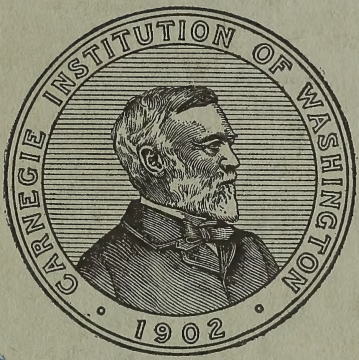
PUBLISHED PAPERS AND ADDRESSES OF JOHN CAMPBELL MERRIAM

VOLUME I



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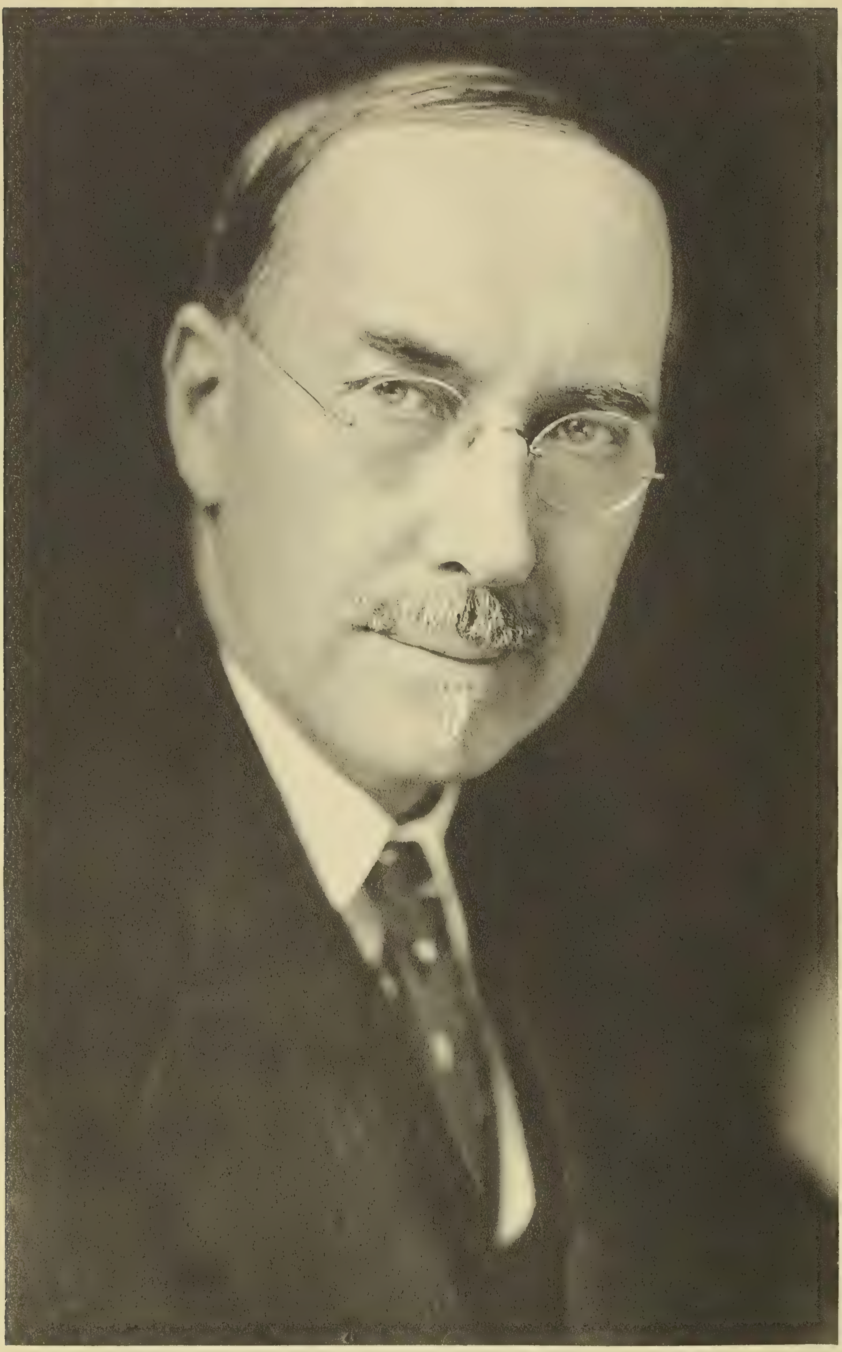

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VOLUME I

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FOREWORD

Believing that a distinct contribution to knowledge may be made by proper presentation of the collected works of a great investigator, the Trustees of the Carnegie Institution of Washington have arranged for the assembling and reprinting of the papers, monographs, reports, lectures, and addresses of John Campbell Merriam. In this series are gathered together his many publications grouped according to general subject, together with a bibliography arranged chronologically. Thus there will be found in these volumes a record of research in palæontology, Dr. Merriam's chosen field, with clear evidence of well-planned investigative program and of superb achievement in the comparative anatomical, particularly vertebrate, aspects of this widely radiating branch of biological thought. Here in these volumes will be found not only this continuing tale of investigative accomplishment along a single line of endeavor but also the occasional digression, the opportunistic following of a research lead, which constitutes a fascinating sidelight upon the workings and mental processes of a biologist who can be truly said to be a senior in the profession. Here also will be found a series of addresses dealing broadly with the relationship of science to human existence and happiness; addresses dealing with nature and natural resources in their effect upon human thought. And here will be found discussion of university opportunities and academic responsibilities—the measured thoughts of a scientist who for eighteen years successfully bore the heavy executive functions of a foundation supporting research in many of the overlapping divisions of human knowledge.

The Trustees of the Carnegie Institution of Washington are glad to acknowledge their debt of gratitude to Dr. John Campbell Merriam, who has served them so effectively as President of the Institution these many years. Coming to the Institution from an important post in a great university, Dr. Merriam brought administrative experience and understanding, outstanding charity and kindness in his relations to staff members and employees alike,

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amazing appreciation of the possibilities for advance in knowledge in the many fields of science and the humanities, and extraordinary abilities and wisdom in the choice of men and projects. A rare investigator, a thoughtful and forceful philosopher in science, a sagacious organizer of successful cooperative undertakings in research, an ardent expositor of the value of original investigation to the general public, a wise leader—Dr. Merriam has made notable contribution to human progress and well being; the Trustees of the Institution feel that these volumes of Dr. Merriam's publications and addresses witness this contribution.

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REPTILIA

UEBER DIE PYTHONOMORPHEN DER KANSAS-KREIDE

Mit Tafel I–IV und 1 Abbildung

Literatur

Baur, G.: On the morphology of the Skull in the Mosasauridae. Journal of Morphology Vol. VII. Oct. 1892. p. 1–23.

Cope, Edw.: On the Reptilian orders Pythonomorpha and Streptosauria. Proceed. Boston Soc. nat. hist. 1869. XII. p. 250.

Cope, Edw.: Synopsis of the extinct Batrachia, Reptilia and Aves of North-America. Trans. Americ. Philos. Soc. Philad. 1871 V. XIV.

Cope, Edw.: Rep. U. S. geol. Surv. of Terr. 1875, Vol. II. The Vertebrata of the cretaceous Formations of the West p. 113–178 and p. 264.

Cope, Edw.: Professor Owen on Pythonomorpha. Bulletin of the U. S. geol. and geograph. Survey of Territor. 1878. Vol. IV. p. 299–311.

Cuvier, G.: Rech. sur les ossem. foss. 4 ed. t. X. p. 119.

Dollo, L.: Note sur l'ostéologie des Mosasauridae. Bull. Roy. d'hist. nat. de Belgique 1882. t. I.

Dollo, L.: Première note sur le Hainosaure. Ibid. 1885. t. IV.

Dollo, L.: Sur le crâne des Mosasauriens in Giard. Bull. scient. de la France et de la Belgique 1888 ser. I.

Dollo, L.: Première note sur les Mosasauriens de Mesvin. Bull. de la Société Belge de Geologie, Paleontologie et d'Hydrologie t. III. 1889.

Dollo, L.: Première note sur les Mosasauriens de Maestricht. Ibidem t. IV. 1890.

Goldfuss: Nova acta Acad. Leopold. Carol. Bd. XXI.

Gaudry, Albert: Les Pythonomorphes de France. Memoires de la Société geologique de France. Memoire No. 10. 1892.

Hector, J.: On the Fossil Reptilia of New Zealand. Trans. and Proceed. of New Zealand Institut 1873. Vol. IV. p. 351.

Knight, C.: On the Teeth of the Leiodon. Trans. and Proceed. of New Zealand Inst. 1873. Vol. IV. p. 358.

Leidy, Jos.: Cretaceous Reptiles of the U. S. Smithson. Contrib. 1864.

Leidy, Jos.: Rep. U. S. geol. Survey of Territ. I. Extinct Vert. Fauna of the Western Territories. Washington 1873.

Marsh, O.: Notice of some new Mosasauroid Reptiles from the Greensand of New Jersey. Am. Journ. of Science 1869, No. 144. p. 392.

Inaugural-Dissertation zur Erlangung der Doctorwürde in der hohen philosophischen Facultät der Ludwig-Maximilians-Universität zu München. *Palaeontographica*, vol. 41, pp. 1–39, pls. I–IV, 1894.

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Marsh, O.: On some new fossil Reptiles from the Cretaceous and Tertiary Formations. Amer. Journ. Sc. and arts 1871. Bd. 101. p. 449.
Marsh, O.: On the Structure of the Skull and Limbs in Mosasauroid Reptiles. Ibid. 1872. Bd. 103. p. 448.
Marsh, O.: New Characters of Mosasauroid Reptiles. Ibid. 1880. Bd. 19. p. 83.
Owen, Richard: On the rank and affinities of the Mosasauridae. Quart. journ. geol. Soc. 1877. Bd. 33. p. 682.
Owen, Richard: On the affinities of the Mosasauridae. Ibid. 1878. Bd. 34. p. 748.
Owen, Richard: Odontographie p. 261.
Williston and Case: Kansas Mosasaurs. Part. I. Kans. Univ. Quarterly Vol. I. July 1892. p. 15.
v. Zittel, Karl A.: Handbuch der Palaeontologie, Abth. I. Bd. III, S. 611.

Einleitung

Unter den fossilen Reptilien bilden die Mosasauriden oder Pythonomorphen, wie sie von E. D. Cope genannt wurden, eine der interessantesten Gruppen, nicht nur weil ihre Entdeckung bis zu einem gewissen Grad den uralten Sagen von Meerschlangen und ähnlichen Ungeheuern eine thatsächliche Unterlage bietet, und einen Blick in den eigenartigen Haushalt der Natur zur Kreidezeit gewährt, sondern auch, weil die genaue Kenntnis ihrer Osteologie mancherlei wichtige Thatsachen über die Entwicklungs- und Verwandtschaftsbeziehungen der Reptilien im Allgemeinen zu Tage gefördert hat. Dem ersten Vertreter der Mosasauriden, welcher schon am Ende des vorigen Jahrhunderts in Maestricht aufgefunden wurde, folgten von Zeit zu Zeit in verschiedenen Welttheilen neue Reste dieser interessanten Familie und bis jetzt hat man in Belgien, Frankreich und England, in den Ost-, Süd- und West-Vereinigten Staaten und Neuseeland so zahlreiche Funde gemacht, dass man daraus fast vermuthen möchte, die Mosasauriden hätten während der Kreidezeit in allen Meeren ihre Beute verfolgt und ihre Ueberreste würden mit der Zeit auch noch in anderen Ländern, wo die Kreide entwickelt ist, zum Vorschein kommen.

Das Material, welches den Gegenstand dieser Studien über die Pythonomorphen von Kansas bildet, wurde zum Theil i. J. 1890 von Dr. G. Baur und zum Theil in den Jahren 1891–92 von Charles M. Sternberg in den Niobraraschichten der oberen Kreide von Logan County, Kansas gesammelt und von Professor K. A. v. Zittel für das palaeontologische Museum in München erworben.

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In dieser Sammlung befinden sich ausser zahlreichen Theilen von Schädeln, Extremitätenknochen und Reihen von Wirbeln, von *Platecarpus* sieben, von *Tylosaurus* (*Liodon*) vier und von *Clidastes* drei fast vollkommene Schädel mit dazugehörigen Wirbelsäulen und theilweise auch Extremitäten, so dass man im Stande ist, die Osteologie dieser Thiere in einer Vollständigkeit darzulegen, wie sich früher die Gelegenheit nie geboten hat.

Die obere Kreide im westlichen Theile der grossen Centralebene der Vereinigten Staaten wird jetzt meistens in die Dakotah-, Colorado- und Foxhill-Gruppen gegliedert. Die Coloradogruppe wird oft weiter in die Unterabtheilungen der Benton-, Niobrara- und Pierre-Gruppen zerlegt. Die Niobraragruppe, in welcher die Ueberreste der Mosasauriden vorkommen, entspricht ungefähr der mittleren Kreide Europa's. Sie besteht petrographisch aus einer weichen gelben Kreide, die nach unten in einen bläulichen Mergel übergehen kann. Besonders die bläulichen Schichten sind oft reich an Krystallen und dünnen Schichten von Gyps, der zuweilen die Fossilien bedeckt uud ihre Präparation sehr erschwert. Die Niobrara-Gruppe enthält nicht sehr viele Ueberreste von Invertebraten, ist dagegen reich an Wirbelthier-Resten. Von characteristischen Mollusken sind *Haploscapha grandis*, *H. excentrica*, *Inoceramus problematicus* und *Ostrea congesta;* von Echinodermen ein sehr characteristischer Crinoid, *Uintacrinus socialis* zu erwähnen. Von Wirbelthieren, die durch zahlreiche Species vertreten sind, führen wir ausser den später beschriebenen fünf Gattungen der Pythonomorphen folgende besonders häufige oder characteristische Formen auf, und zwar von Vögeln: *Hesperornis regalis*, *Ichthyornis dispar*, *Ichthyornis celer;* von Reptilien: *Pteranodon occidentalis*, *Pteranodon umbrosus*, *Hadrosaurus minor*, *Elasmosaurus platyurus*, *Protostega gigas;* von Fischen: *Ptychodus occidentalis*, *Otodus divaricatus*, *Lamna cuspidata*, *Portheus molossus*, *Ichthyodectes polymicrodus.*

Aufrichtigen und warmen Dank schulde ich Herrn Dr. I. Böhm in München für die bereitwillige und freundliche Hilfe, die er mir bei der Fertigstellung meines Manuscriptes geleistet. Meinem hochverehrten und geschätzten Lehrer Herrn Professor Dr. von Zittel aber gebührt mein wärmster Dank für das ausgezeichnete, mir zur Arbeit gegebene Material, für seinen allzeit freundlichen und guten Rath und die besondere Theilnahme, die er mir während meiner Studien in München angedeihen liess.

GESCHICHTLICHES

Der erste Vertreter der Thiergruppe, die den Inhalt dieser Arbeit bildet, gehört der Gattung *Mosasaurus* an. Er wurde i. J. 1780 von einem Garnisons-Chirurgen HOFMANN in Maestricht für seine Fossiliensammlung von den Arbeitern in den Steinbrüchen des Petersberges[1] bei Maestricht erworben. Jedoch nicht lange erfreute er sich dieses Besitzes, da ein Canonicus, dem der Boden, unter welchem der Steinbruch lag, gehörte, den Schädel für sich beanspruchte und schliesslich durch das Gericht zugesprochen erhielt. Als die französischen Truppen i. J. 1795 die Festung auf dem Petersberg bombardirten, liessen sie zwar das Haus, in welchem der General den berühmten Schädel vermuthete, unversehrt, wurden aber nach Uebergabe der Stadt in ihren Hoffnungen auf seinen Besitz enttäuscht, da der Canonicus das Fossil während der Belagerung versteckt hatte. Die auf diesen Fund ausgesetzte Belohnung von 600 Flaschen Wein hatte zur Folge, dass der Schädel am andern Tag zum Vorschein kam. Er wurde später nach Paris gebracht und befindet sich jetzt dortselbst im Jardin des plantes. CONYBEARE stellte zuerst den Namen *Mosasaurus* für dieses Fossil auf, CUVIER[2] hat ihn 1808 abgebildet und sorgfältig beschrieben. Er wies auf die grosse Aehnlichkeit mit *Monitor* hin und diese Auffassung seiner systematischen Stellung hat sich jetzt als vollständig gerechtfertigt erwiesen.

Im Jahre 1844 beschrieb GOLDFUSS[3] eingehend den Schädel und die Wirbelsäule eines Mosasauriden aus Nord-America, dem er den Namen *Mosasaurus Maximiliani* beilegte. Diese Beschreibung ist bis in die jüngste Zeit die beste geblieben. Das Skelet, welches von einem Agenten der Indianer des oberen Missouri in der Nähe des Bigbend gefunden wurde, brachte der Prinz MAXIMILIAN ZU WIED aus America mit und schenkte es dem Museum zu Bonn. Der Schädel ist beinahe vollständig. GOLDFUSS hat fast jedem Theil die richtige Lage und auch die Beziehungen zu den andern Knochen richtig angegeben. Auf seinen schönen Abbildungen sieht man das Quadratum, Pterygoid, Palatinum, Prooticum, Parietale und Lacrymale, die später der Gegenstand eingehender Discussionen gewesen sind, sorgfältig dargestellt, so dass durch seine Monographie die Kenntniss der *Mosasaurus*-Osteologie wesentlich gefördert wurde.

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[1] Faujas de Saint-Fond. Hist. de la Montagne de Saint-Pierre p. 59.

[2] Rech. sur. les ossem. foss. 4 ed. t. X. p. 119.

[3] Der Schädelbau des Mosasaurus. Nova acta. Acad. Leopold. Carol. Bd. XXI.

Im Jahre 1869 stellte Cope[4] die Ordnung der Pythonomorphen auf, der er im System ihre Stellung zwischen den Eidechsen und den Schlangen anwies. Von den 17 Merkmalen dieser Ordnung fand er 10 bei den Schlangen und 5 bei den Eidechsen wieder; 2 derselben fasste er als dieser neuen Ordnung eigenthümlich auf. Im Jahre 1875[5] characterisirte er die Ordnung zum zweiten Male; unter den sieben Ordnungsmerkmalen treffen jedoch zwei nicht zu.

Im Jahre 1877 erörterte Owen[6] sehr ausführlich die Osteologie der Mosasauriden mit Rücksicht auf ihre Verwandtschaft mit den Eidechsen und Schlangen und auf ihre Recht als selbstständige Ordnung zu gelten. Er griff Cope's Ansichten an und erklärte sich entschieden für die Zutheilung der Mosasauriden zu den Eidechsen, da sie in den wichtigsten Merkmalen mit dieser Gruppe übereinstimmten und sich nur dadurch von den Lacertiliern unterschieden, dass ihre Extremitäten als Flossen ausgebildet seien. Sie verhielten sich zu den übrigen Eidechsen genau wie die mit flossenartigen Extremitäten versehenen Pinnipedier zu den echten fissipeden Carnivoren. Diese Ansicht suchte Owen in einem zweiten Artikel[7] weiter zu begründen, worin er speziell auf die vergleichende Osteologie der Flossen einging und auf ihre grössere Aehnlichkeit mit den Extremitäten der Lacertilier als mit denen der Cetaceen oder Sauropterygier hinwies.

In seiner Erwiederung hat Cope[8] 1878 die Ordnung Pythonomorpha erneut characterisirt und ihre Selbstständigkeit Owen gegenüber vertheidigt.

Zwischen den Jahren 1869 und 1880 liess Marsh[9] als Frucht seiner Studien eine Reihe wichtiger Abhandlungen über die Pythonomorphen erscheinen, worin er die Entdeckung der Hinterextremitäten, des Stapes, der Columella, des Transversum, Sternum und Hyoideum veröffentlichte. Ehe Marsh die Hinterextremitäten entdeckte, wurde ihre Abwesenheit sogar als ein Ordnungs-Merkmal benutzt.

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[4] On the Reptilian Orders Pythonomorpha and Streptosauria. Proceed. Boston. Soc. nat. hist. 1869. XII. p. 250.

[5] Vertebrata of cretaceous Formations of the West. p. 113–178 and p. 264.

[6] Quart. journ. geol. Soc. 1877. Bd. 33 p. 682.

[7] On the affinities of the Mosasauridae. Ibid. 1878. Bd. 34. p. 748.

[8] Bull. U. S. Geol. and Geogr. Surv. of Territ. 1878. Vol. IV. p. 299.

[9] Siehe Literatur.

Im Jahre 1892 erschienen zwei wichtige Abhandlungen; in der einen machten uns WILLISTON and CASE[10] mit der Wirbelsäule und den Extremitäten von *Clidastes* genauer bekannt, in der zweiten beschrieb BAUR[11] den Schädel von *Platecarpus*. Mit diesen beiden Schriften erfuhr die Kenntniss der americanischen Pythonomorphen einen ausserordentlichen Fortschritt.

Die Vermehrung unserer Kenntnisse der europäischen Mosasauriden verdanken wir ausser CUVIER hauptsächlich DOLLO und in letzter Zeit GAUDRY. DOLLO[12] stellte zwischen 1882 und 1890 die Genera *Plioplatecarpus*, *Pterycollosaurus*, *Hainosaurus*, *Proterognathus*, *Phosphorosaurus* und *Oterognathus* auf. Der Name *Pterycollosaurus* wurde für *Mosasaurus Maximiliani* von GOLDFUSS geschaffen und derselbe auf Grund seiner in der Mittellinie verwachsenen Pterygoidea zum Typus einer neuen Gattung erhoben. Es hat sich jedoch herausgestellt, dass diese Verwachsung nur eine scheinbare ist, durch Zusammenpressen der Flügelbeine hervorgerufen. Das Genus *Plioplatecarpus* beruht hauptsächlich auf der Verwachsung zweier Wirbel zur Bildung des Sacrum's. Es ist aber wahrscheinlich, dass die Verwachsung als eine pathologische Erscheinung betrachtet werden muss. Ausser den erwähnten und von DOLLO aufgestellten Gattungen hat er noch das Genus *Mosasaurus* eingehend beschrieben und besser characterisirt als die früheren Autoren.

GAUDRY[13] beschrieb im Jahre 1892 die Pythonomorphen Frankreichs, wobei er die sehr schön erhaltenen Vordertheile zweier Mosasaurier-Schädel besprach und sie zur Gattung *Liodon* OWEN stellte. Damit gab er endlich dem OWEN'schen Genus, welches nur auf fragmentarischen Ueberresten begründet war, eine Unterlage.

Von grossem Interesse ist ferner der Fund von Pythonomorphenresten in Neuseeland, die 1873 von HECTOR[14] beschrieben wurden. Dieser Autor stellte einen Theil derselben zu *Liodon*, einen anderen Theil zu einer neuen Gattung *Taniwhasaurus*.

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[10] Kansas Univ. Quart. Vol. I. July 1892. p. 15.

[11] Journal of Morphology Vol. VII. Oct. 1892. p. 1.

[12] Siehe Literatur.

[13] Memoires de la Société geologique de France. Memoire Nr. 10. 1892.

[14] Trans. and Proceed. of New Zealand Institut. 1873. Vol. VI. p. 351.

ALLGEMEINE BESCHREIBUNG

Von den bis jetzt aus verschiedenen Welttheilen bekannten Pythonomorphen-Gattungen (*Mosasaurus*, *Hainosaurus*, *Liodon*, *Plioplatecarpus*, *Prognathosaurus*, *Phosphorosaurus*, *Oterognathus*, *Taniwhasaurus*, *Platecarpus*, *Clidastes*, *Tylosaurus*, *Baptosaurus* und *Sironectes*) kommen *Platecarpus*, *Clidastes*, *Tylosaurus*, *Baptosaurus* und *Sironectes* in den Niobraraschichten der Kansas-Kreide vor. Nach WILLISTON and CASE finden sich *Platecarpus* und *Tylosaurus* (*Liodon*) schon in der unteren, *Clidastes* nur in der obersten Abtheilung dieses Horizontes. Von diesen drei Gattungen haben WILLISTON and CASE die Wirbelsäule und Extremitäten von *Clidastes* ausführlich beschrieben und vor Kurzem hat BAUR die einzelnen Knochen des Taf. I Fig. 1, 2 abgebildeten, wundervoll erhaltenen Schädels von *Platecarpus coryphaeus*, welcher sich im Münchener Museum befindet, genau erörtert und abgebildet, so dass in dieser Abhandlung von diesen beiden Gattungen nur die wichtigeren Merkmale angegeben sind, während *Tylosaurus*, dessen Osteologie noch nicht genau untersucht worden ist, möglichst detaillirt beschrieben wurde.

Die äussere Form der Mosasauriden war, wie der in mancher Hinsicht glücklich gewählte Name *Pythonomorpha* ausdrückt, schlangenartig, wobei jedoch kurze flossenartige Extremitäten, die im Aeusseren wohl viel Aehnlichkeit mit denen von *Ichthyosaurus* besessen haben, vorhanden waren und bei der Locomotion dem Thiere, zusammen mit dem langen, horizontal zusammengedrückten, breiten Schwanz, eine ausgezeichnete Schwimmfähigkeit verliehen haben. Der Rumpf war lang und schlank, der Hals kurz, aber nach allen Richtungen leicht beweglich, der Kopf, besonders bei *Clidastes* und *Tylosaurus* länglich, mit grossen Augen, die wie bei *Ichthyosaurus* mit einem Scleroticaring versehen waren. Der weit dehnbare Rachen war mit langen, kräftigen Zähnen bewaffnet und auch im hinteren Theil des Gaumens trugen die beiden langen Flügelbeine scharf zugespitzte und gekrümmte Zähne. Die Haut war wahrscheinlich nackt, wenigstens sind bis jetzt keine knöchernen Hautbildungen aufgefunden worden.

Die Gebilde, welche anfänglich für Hautplatten gehalten wurden, haben sich später als Scleroticaplatten herausgestellt.

Die Wirbelsäule, die aus circa 120 procoelen Wirbeln bestand,

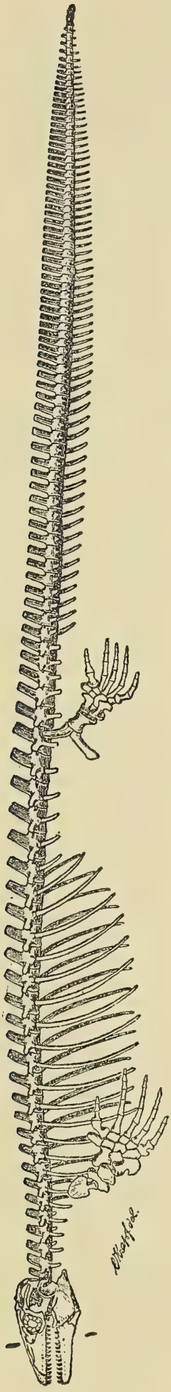

Fig. 1. *Platecarpus coryphaeus* Cope. Restaurirtes Skelet. (Limbs in part from other forms)

war infolge der Ausbildung der Extremitäten und der beiden die Extremitäten stützenden Gürtel in deutlich markirte Hals-, Rumpf- und Schwanzabschnitte getheilt, wobei Lendenwirbel zu fehlen scheinen, da die Rippen sich wahrscheinlich bis zum Beckengürtel fortsetzten; diejenigen Wirbel, die für Lendenwirbel gehalten worden sind, gehören dem Schwanzabschnitte an und sind von Williston and Case Pygialwirbel genannt worden. Von dem Atlas sind die beiden Seitenstücke und ein längliches, viereckiges Basalstück frei, während der Processus odontoideus und die dazu gehörige Hypapophyse meistens ziemlich eng mit dem Epistropheus verwachsen sind. Die Halswirbel besassen starke, mit dem Centrum verschmolzene Bogen und grosse Hypapophysen, die meistens mit einem separat abgegliederten Endstück versehen waren. Es konnte jedoch das Endstück mit dem Centrum verwachsen, wie dies bei *Baptosaurus* und ziemlich häufig auch bei *Clidastes* vorkommt. Auch waren bei allen Halswirbeln stärkere oder schwächere Zygapophysen und bei den meisten Gattungen Zygosphen, Taf. III Fig. 9, 11, oder Andeutungen davon vorhanden. Die Rückenwirbel, die keine gegliederten Hypapophysen zeigten, hatten, wie auch die Halswirbel, mit Ausnahme des Atlas, einköpfige Rippen, die am Thorax durch Knorpel mit dem Sternum verbunden waren. Vom Brustkorb aus nach hinten wurden die Rippen allmählich kürzer und hörten unmittelbar vor dem Beckengürtel auf. Die ersten Schwanzwirbel besassen breite Diapophysen und keine Haemapophysen und wurden, wie oben erwähnt, mit dem Namen Pygialwirbel belegt. Hinter den Pygialwirbeln hatten die Schwanzwirbel Chevron-Bones (geschlossene Haemapophysen), die zuweilen (*Clidastes*) mit dem Centrum verwuchsen, meistens jedoch frei blieben. Der Schultergürtel ist nach dem Vorbild der Eidechsen gebaut und zeigt eine Scapula und ein Coracoideum, die der Form nach mit denen der Lacertilier übereinstimmen. Die Coracoidea verband ein dünnes, wahrscheinlich durch Einlagerungen von kohlensaurem Kalk verstärktes Sternum, das durch breite Knorpelbänder mit den Thoracalrippen verbunden war. Auch der Beckengürtel unterscheidet sich sehr wenig von dem der Lacertilier, das Ileum war lang und schlank, das Schambein etwas schmäler, und das Sitzbein etwas breiter, als bei den meisten Eidechsen. Auch haben die Flossen einen ausgesprochenen lacertilen Bau, unterscheiden sich jedoch nicht unerheblich dadurch, das Humerus und Femur, Radius, Ulna, Tibia und Fibula alle verkürzt und verflacht sind. Die Zahl der Phalangen war für die Vorder- und Hinterextremitäten annähernd 3 5 5, 4 3, steht also sehr nahe der Zahl der Phalangen bei den Varaniden.

Der Schädel, Taf. I, II, war länglich, vorn, besonders bei *Tylosaurus* und *Clidastes* spitzig und hatte seitwärts gerichtete Augen und lange, etwas nach hinten gerückte obere Nasenlöcher. Die unpaarige Praemaxilla erstreckte sich in einem langen Stiel nach hinten, der am Hinterende mit den Nasalien verschmolz und sich an das spitze Vorderende des Frontale anlegte. Die Maxillen, wie auch die beiden Zahnbeine waren lang, schmal und je nach den Gattungen mit 12 bis 17 Zähnen besetzt, während das Dentale 12 bis 18 Zähne besitzen konnte.

Vorn, zwischen den Maxillen und gegen den bezahnten Theil des Praemaxillare anstossend lagen die Vomer, die nach hinten auseinander gingen und mit zwei langen, stielartigen vorderen Fortsätzen der Palatina in Verbindung standen. Wie bei den Eidechsen lagen vorn auf dem Vomer die Turbinalia, welche die länglichen Nasenlöcher vorne schliessen. Das Frontale war wie das Parietale unpaarig, zeigte jedoch vorne einen Rest der die beiden Hälften wohl in der Jugend trennenden Sutur. Die Praefrontalia, die bei den verschiedenen Gattungen beträchtlich differiren, ruhten auf den Palatinen und legten ihre Vorderenden auf die Innenseite des Hinterendes des Maxillare. Ob ein mit dem Praefrontale verbundenes Superciliare vorhanden war, ist zweifelhaft, jedenfalls war es dann zu einer kleinen, dreieckigen Platte auf der Aussenseite der Praefrontale verkümmert.

Die von Baur als Superciliare[15] gedeuteten Knochen sind die Transversa. Ein kleines Thränenbein dürfte, wir schon Goldfuss gezeigt hat,[16] überall vorhanden gewesen sein. Die grossen, seitlich gelegenen Augenhöhlen wurden vom Praefrontale, Lacrymale, Jugale und Postfrontoorbitale begrenzt; bei einigen Gattungen nahm auch das Frontale Theil an der Begrenzung, während bei anderen, besonders bei *Tylosaurus* das Postfrontale sich über die Aussenseite der Praefrontalia geschoben und so das Frontale von der Begrenzung ausgeschlossen hat.

Die Palatina, die mit dem Hinterende der Maxillen in Berührung kamen, stiessen nicht in der Mitte zusammen, sondern waren durch einen kleinen Zwischenraum getrennt. Sie waren vorn mit den Vomern, hinten mit den Flügelbeinen durch Sutur verbunden. Die Pterygoidea, die in ihrer Form grosse Aehnlichkeit mit denen von *Varanus* besassen, jedoch grosse Zähne trugen, waren durch Ligament mit dem Quadratum und durch Sutur mit Palatinum und Transversum verbunden. Das von Prof. Marsh entdeckte Transversum[17] war nach ihm ein langer L-förmiger Knochen, der mit dem Ectopterygoidal-Fortsatz des Pterygoids durch seinen kurzen Ast verbunden war, während der längere, nach vorn und hinten stehende Ast mit seinem Vorderende an das Hinterende der Maxillare stiess. Nach Prof. Marsh soll bei *Platecarpus* (*Lestosaurus*) eine Columella (Epipterygoid) wie bei den Eidechsen vorhanden sein und an einem der mir vorliegenden Exemplare finden sich zwei Knochen, die in der That kaum anders als Columella gedeutet werden können.

Das Postfrontoorbitale, das mit dem Quadratojugale, den Schläfenbogen bildete, schickte einen kurzen Fortsatz nach unten aus, der mit dem Jugale zusammenstiess und einen vollständigen Jochbogen bildete, wobei Jugale und Quadratojugale sich auf der Unterseite des Postfrontale berührten.

Das Scheitelbein, das mit zwei von den Seiten herunterhängenden Lappen auf den Prootica und dem Occipitale superius ruhte, sandte zwei divergirende Arme nach hinten aus, die mit den nach oben und vorn gerichteten Aesten der Squamosa verbunden waren und mit letzteren die Quadratoparietalbogen bildeten. Das Scheitelloch auf dem Vordertheil des Parietale variirte bezüglich der Grösse und Nähe zur Coronalsutur bei den verschiedenen Genera.

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[15] Journ. Morph. Vol. VII. Oct. 1892, p. 15.

[16] Nova Acta. Acad. Leopold. Carol. Bd. XXI. p. 182.

[17] Amer. Journ. Science and Arts. 1872, p. 449.

Die Gehirnkapsel war vorn weit offen, im Gegensatz zu derjenigen der Schlangen, mit der sie verglichen worden ist; sie hat die grösste Aehnlichkeit mit der Gehirnkapsel der Eidechsen. Das Prooticum, das am Vorderrand tief ausgeschnitten ist, streckt sich nach hinten aus bis zur Mitte des nach hinten gerichteten Armes des Ex-Occipitale und stösst hier an das Vorderende des Unterastes vom Squamosum.

Das Basisphenoid stösst hinten an das Basioccipitale und trägt auf seiner Oberseite die Prootica. Vorn schickt es einen langen sehr schmalen Fortsatz, das Praesphenoid, aus. Das Basisphenoid ist ausgesprochen eidechsenartig, ähnelt sehr dem der Varaniden und hat wie bei diesen auf der Unterseite keine Carina. Das Basioccipitale, das den Hauptheil des Gelenkkopfes bildet, läuft unten in zwei grosse Hypapophysen aus, die mit ihrer Vorderseite gegen das Basisphenoid stossen. Das Occipitale superius ist oben in einen mehr oder weniger hohen Kamm verlängert und nimmt hinten in einer Einkerbung auf demselben die beiden hinten verwachsenen Lappen des Parietale auf. Die mit den Opisthotica verschmolzenen Occipitalia lateralia verlängern sich hinten in zwei lange, seitlich zusammengedrückte Arme, die auf ihrer Aussenseite vom Prooticum und Squamosum bedeckt sind. Auf der Aussenseite des Hinterendes dieses Armes liegt das Squamosum, das aus zwei Aesten besteht, wovon der eine, wie schon oben bemerkt, auf dem Arm des Occipitale laterale liegt, während der andere nach oben und vorn ausgeht und mit dem Parietalprocessus den Quadratoparietalbogen bildet. Das Squamosum ist da, wo die beiden Aeste zusammenstossen, ausgehöhlt und bildet mit dem auf seiner Aussenseite liegenden Kopf des Quadratojugale die Gelenkpfanne für das proximale Ende des Quadratum.

Wie bei den Schlangen und Eidechsen war das Quadratum gelenkig mit dem Schädel verbunden, unterscheidet sich aber durch seine Gestalt von den Quadratbeinen aller anderer Reptilien. Der Aussenrand der Vorderseite erweitert sich immer zu einem Flügel, der bei den verschiedenen Gattungen sehr verschieden ist, bei einigen sehr breit und in der Mitte dünn, bei anderen kurz und dick. Ueber dem Meatus auditorius wird das Oberende des Quadratum nach hinten und unten in einen mehr oder weniger langen, hakenartigen Fortsatz ausgezogen, den DOLLO Supracolumellar-Fortsatz (Apophyse supracolumellaire) genannt hat. Unter dem Meatus auditorius ist meistens eine leistenartige Erhöhung vorhanden, die bei einigen europäischen Gattungen mit dem Supracolumellar-Fortsatz in Berührung steht und den Meatus vollständig umschliesst; bei den americanischen Gattungen ist jedoch bis jetzt kein Fall angeführt worden, wo diese Erhöhung mit dem oberen Fortsatz zusammenstösst. Auf der Innenseite des Quadratum befand sich eine kleine Grube (Stapedialgrube) in die sich ein langer schlanker Stapes einfügte.

Am Unterkiefer wurde die Gelenkpfanne für das Quadratum von Articulare und Supraangulare gebildet. Der Unterkiefer, der aus Articulare, Angulare, Supraangulare, Coronoideum, Dentale und Operculare besteht, stimmt im allgemeinen Bau mit dem der Eidechsen überein, unterscheidet sich jedoch dadurch, dass zwischen Operculare und Angulare ein wohlentwickeltes Gelenk ausgebildet ist, infolge dessen die hinteren und vorderen Theile des Kiefers gegeneinander wie bei den Schlangen, einen gewissen Grad von Beweglichkeit besassen. Die Mandibeln waren in der Symphyse nur durch Ligament verbunden.

Die grossen und kräftigen Zähne der Pythonomorphen sassen immer auf grossen, aus einer cementähnlichen Knochensubstanz bestehenden Sockeln, die meistens in Alveolen standen; zuweilen aber, wie gelegentlich bei *Platecarpus*, drangen die unteren Enden der Sockel so wenig in den Kiefer hinein, dass die Befestigung fast ebenso acrodont wie thecodont war; auch kommt es vor, dass, besonders bei den Pterygoideen, die Befestigung halb pleurodont wird. Die jüngeren Zähne entstanden auf dem hinteren Theil der Innenseite des Sockels und sobald sie anwuchsen, wurde der Sockel des alten Zahnes allmählich resorbirt und die Krone schliesslich vom jungen Zahn herausgedrängt. Die Krone war hohl, mit einer dünnen Schmelzschicht bedeckt, stark gestreift oder ganz glatt, im Querschnitt entweder rundlich und facettirt oder comprimirt. Sie war an der Basis von dem Sockel umwachsen, ragte ziemlich tief in ihn hinein und blieb um unteren Ende vollkommen offen.

Noch bleibt von den erhaltungsfähigen Hartgebilden der Pythonomorphen zu erwähnen übrig, dass ein Paar Zungenbeine vorhanden war und ferner, dass bei manchen Skeletten unter den hinteren Halswirbeln und auf dem Brustbein eine grosse Anzahl von ringförmigen Gebilden sich fanden, die unzweifelhaft die Trachealringe darstellen. Der Scleroticaring, der schon oben erwähnt wurde, bestand aus vielen, kleinen, dünnen, viereckigen Platten, die übereinandergriffen und einen festen Ring, wie bei *Ichthyosaurus* und *Varanus* bildeten.

Wie aus dem Vorhergehendem erhellt, war der Pythonomorph mit seinem bis zu 50 Fuss langen schlanken Körper, in allen Beziehungen für die Verfolgung und den Fang seiner Beute ausgerüstet und somit einer der gefährlichsten Räuber des Meeres zu der Zeit, in der er lebte. Dass sein Dasein kein friedliches war, geht daraus hervor, dass manche der uns überlieferten Knochen geheilte Bissnarben zeigen, als unzweifelhaftes Zeichen eines heftigen Kampfes. Diese Bissnarben dürfen jedoch nicht mit der Erscheinung verwechselt werden, dass oft lange nach dem Tode des Thieres durch den Gebirgsdruck die Zähne eines Kiefers oder Flügelbeines in die weich gewordene Knochensubstanz eines anderen Knochens gepresst wurden.

Von den vier Gattungen *Clidastes*, *Platecarpus*, *Tylosaurus* und *Sironectes* weist die kleinsten Repräsentanten der Familie das Genus *Clidastes* auf, bei welchem Individuen mit einer Schädellänge von 22 cm vorkommen. Der *Clidastes*, Taf. I Fig. 4 war schlanker, leichter gebaut und im Aeusseren schlangenartiger als die anderen. Der Kopf war lang und schmal mit spitz ausgezogener Schnauze, die etwas über die Mandibelspitzen vorragte, die Kiefer lang und schlank mit 18 Zähnen auf dem Dentale, 17 auf dem Maxillare und 2 auf jeder Seite der Praemaxilla. Auch waren die Flügelbeine mit ihren langen Reihen gekrümmter Zähne, die sich von einem Punkt neben dem Hinterende des Oberkiefers bis hinter die Augenhöhlen erstreckten, länger als bei den andern Gattungen und besassen 15 Zähne gegen 12 und 11 bei *Platecarpus* und *Tylosaurus*. Der Hals war kurz und die sieben Wirbel mit starken Zygapophysen und Zygosphen versehen. Der Rumpfabschnitt enthielt im Gegensatz zu *Tylosaurus* und wahrscheinlich auch zu *Platecarpus* 35 Wirbel und machte ungefähr 40% der ganzen Körperlänge von der Schnauzenspitze bis zum Ende des Schwanzes aus. Der Schwanzabschnitt war infolge der Verlängerung des Rumpfes verhältnissmässig kurz, bestand aus 74 Wirbeln und nahm etwa 42% der Körperlänge ein. Auch unterscheiden sich die Schwanzwirbel von denen der anderen Kansas-Pythonomorphen dadurch, dass die

Haemapophysen (Chevron-Bones) mit den Wirbelcentren fest verwachsen waren.

Die Gattung *Tylosaurus*, Taf. I Fig. 3, Taf. II weist im Gegensatz zu *Clidastes* die grössten Repräsentanten der vier Gattungen auf. Die kleinsten Species besassen wohl selten eine Schädellänge von weniger als 70 cm, während die grössten Individuen enorme Dimensionen bis zu 15 m erreichten. Die Schnauze von *Tylosaurus* war, wie bei *Clidastes*, vor dem ersten Zahnpaar schnabelartig verlängert, nur viel ausgesprochener als bei letzterem, und war am Ende nicht zugespitzt, sondern gerade abgestutzt. Die Kiefer waren lang und schmal, aber nicht so leicht gebaut wie bei *Clidastes* und trugen am Dentale und auf dem Maxillare je 13 Zähne. Das Frontale war mit vielen länglichen, vom Scheitelloch nach vorn ausstrahlenden Gruben verziert. Das Quadratum endigte im Gegensatz zu *Platecarpus* mit einem kurzen spitzen Supracolumellar-Fortsatz. Auf den kurzen Hals, dessen Wirbel nur eine Andeutung von Zygosphen zeigten, folgte ein kurzer Rücken, der 23 Wirbel enthielt und etwa 23% der Körperlänge ausmachte. Der Schwanz wird infolge der Verkürzung des Rückens 12% länger und enthält 87 Wirbel. An den Caudalwirbeln von *Tylosaurus* waren die Chevron-Bones, die bei *Clidastes* mit den Wirbelcentren verwuchsen, gelenkig verbunden.

Der *Platecarpus*, Taf. I Fig. 1, 2, dessen Reste unter den in Kansas vorkommenden Pythonomorphen am häufigsten zu sein scheinen, nähert sich im allgemeinen Bau mehr dem *Varanus* als die anderen Genera. Die Schnauze war breit und am Ende stumpf, sogar zuweilen vorn herzförmig eingeschnitten, auch verjüngt sich der Praemaxillar-Stiel nach hinten viel früher als bei *Tylosaurus* oder *Clidastes*. Die Maxillen waren kurz und breit und wie das Dentale mit 12 facettirten Zähnen besetzt. Die etwas S-förmigen Pterygoidea trugen meistens 12 Zähne. Am Quadratum war der Aussenflügel sehr breit, der Supracolumellar-Fortsatz lang, am Ende breit und gerade abgeschnitten. Das Parietale zeigt bei *Platecarpus* allein auf der Oberseite vorn ein dreieckiges Feld, das über das Niveau der Basis der nach hinten gerichteten Arme heraufragt. Die Halswirbel hatten ein etwas stärkeres Zygosphen als bei *Tylosaurus*, unterscheiden sich aber durch die schwache Entwicklung dieses Theiles des Wirbels mit *Tylosaurus* vom *Clidastes*, bei denen das Zygosphen an den Halswirbeln immer gut entwickelt ist. Die

Rücken- und Schwanzabschnitte scheinen, was die Zahl der Wirbel betrifft, mit *Tylosaurus* übereinzustimmen und wie bei diesem waren auch die Chevron-Bones gelenkig mit den Wirbelcentren verbunden.

Das Genus *Sironectes* beruht nur auf sehr fragmentarischen Resten, einigen Wirbeln und einem Stück vom Unterkiefer. Es unterscheidet sich von *Clidastes* durch die beweglich eingelenkten Chevrons und von *Platecarpus* und *Tylosaurus* durch das ziemlich stark entwickelte Zygosphen.

Systematische Stellung und Verwandtschaft der Mosasauridae

Obwohl der *Mosasaurus* von Maestricht schon von Cuvier als ein sehr naher Verwandter von *Monitor* erkannt wurde, ist seit der Aufstellung der Ordnung der Pythonomorphen[18] durch Prof. Cope Vieles über ihre systematische Stellung geschrieben worden, und obwohl fast alle Autoren bezüglich der Homologien der verschiedenen Knochen übereinstimmen, ist die systematische Stellung der Pythonomorphen selbst noch immer nicht ganz sichergestellt. Als Prof. Cope die Ordnung der Pythonomorpha aufstellte, fasste er sie als eine Ordnung der Streptostylica auf, die ihren Platz zwischen den Lacertiliern und den Ophidiern fände, da sie, obwohl in der Osteologie viel Eidechsenähnliches vorhanden sei, doch auch viele und wichtige Merkmale von Schlangen aufwiesen. Prof. Cope hat jedoch die grosse Uebereinstimmung der Pythonomorpha mit den Lacertiliern, besonders mit den Varaniden, nicht verkannt und drückt sich darüber in folgender Weise aus: "That these reptiles . . . are primarily related to the Lacertilia, secondly to the Ophidia . . . they present more points of affinity to the serpents than does any other order and their nearest point of relationship in the Lacertilia is the Varanidae or Thecaglossa."

Auch scheint im Grunde genommen das Resultat einer sehr eingehenden Discussion über die Frage des systematischen Werthes der Pythonomorphen zwischen Owen[19] und Cope,[20] worin die Verwandtschaft dieser Gruppe mit den Eidechsen und Schlangen in eingehendster Weise behandelt wurde, das zu sein, dass beide die grosse Aehnlichkeit mit den Eidechsen und auch in einigen Punkten mit den Schlangen erkennen.

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[18] Proceed Boston Soc. nat. hist. 1869. XII. p. 52.

[19] Quarterly Journ. Geol. Soc. London 1877 p. 682.

[20] Bull. U. S. Geol. and Geog. Surv. Territ. IV. 1878 p. 299.

Stellt man den Schädel eines *Monitor* und eines *Platecarpus* nebeneinander, so ist man auch von der auffallend grossen Aehnlichkeit beider überrascht. Die Schädel stimmen in ihrem Habitus überein und wenn man genauer in die Details eingeht, findet man, dass fast jeder Knochen wenigstens annähernd die gleiche Gestalt und Beziehungen bei beiden Gattungen hat und dass es grössere Schwierigkeiten bereiten würde, Verschiedenheiten als Aehnlichkeiten zwischen ihnen zu finden.

Als Abweichungen in der Schädelosteologie des *Varanus* vom *Platecarpus* wäre nur folgendes zu erwähnen. Das Quadratum ist länger, schlanker und der Superacolumellar-Fortsatz am proximalen Ende sehr klein. Die Fortsätze des Ex-Occipitale die sich auf die Oberseite der Hypapophyse des Basioccipitale hinüberstrecken, sind sehr breit und vertical abgeplattet. Das Occipitale superius ist oben sehr breit, die Flügelbeine sind unbezahnt.

Wenn man dagegen den *Platecarpus*-Schädel mit einem solchen von *Python* vergleicht, so fällt auf den ersten Blick die grosse osteologische Verschiedenheit der beiden ins Auge. Bei *Python* ist im Gegensatz zu *Platecarpus* die hintere Parthie des Schädels weit in die Länge gestreckt und das Quadratbein seiner Gestalt nach weiter von dem des *Platecarpus* entfernt, als das des *Varanus* von dem des *Platecarpus*. Die Gehirnkapsel ist durch das Zusammenstossen des Basisphenoids, Praesphenoids, Orbitosphenoids, Parietale und Prooticum geschlossen, während sie bei *Platecarpus* vorn weit offen bleibt; die Schläfen-, Joch- und Quadratoparietalbogen sind nicht vorhanden; das Basisphenoid besitzt unten eine hohe Carina und zeigt vertical gestellte Pterygoidalprocessi; und obwohl das Pterygoid wie bei den Pythonomorphen bezahnt ist, trägt doch auch das Palatinum Zähne, was bei den Pythonomorphen nicht der Fall ist. Genug, man könnte eine lange Reihe von Merkmalen anführen, wodurch im Schädel allein die beiden Gruppen der Pythonomorphen und Ophidier sich beträchtlich von einander unterscheiden, während fast das einzige Merkmal, das sie gemeinsam haben und das den Eidechsen nicht zukommt, die hochgradig entwickelte Bezahnung des Pterygoid's ist.

Wenn man die übrigen Skelettheile, Wirbelsäule und Extremitäten der drei Gruppen vergleicht, so findet man wieder zwischen den Eidechsen und Pythonomorphen grosse Uebereinstimmung im Bau des Atlas und der übrigen Wirbel; beim Pythonomorphen-Schultergürtel finden wir Coracoidea wie bei den Lacertiliern durch ein von Einlagerungen von kohlensauren Kalk fest gewordenes Sternum verbunden. Der Beckengürtel ähnelt demjenigen der Eidechsen, weicht jedoch in der Befestigung desselben mit der Wirbelsäule ab, indem kein Sacrum vorhanden war und die Hinter-Extremitäten infolge ihrer Umwandlung in Flossen nur durch Ligament mit den Diapophysen der ersten Pygialwirbel verbunden waren. Im allgemeinen Bau zeigen die Extremitäten einen ausgesprochen eidechsenartigen Charakter, nur sind sie durch Verkürzung in Flossen umgewandelt worden.

Wenn wir jedoch die Schlangen zur Betrachtung heranziehen, so sehen wir, obwohl Aehnlichkeiten in der Wirbelsäule vorhanden sind, dass die Becken- und Schultergürtel nebst den Extremitäten, mit Ausnahme von einigen mangelhaften Resten des Beckengürtels, gänzlich fehlen.

Wenden wir uns zu der Liste[21] der nach Prof. Cope für die Ordnung der Pythonomorphen wichtigsten Merkmale, so finden wir folgende:

1. The Parietal bones are decurved on the sides of the cranium and are continuous with the Alisphenoid and Prootic elements.
2. The Opisthotic is largely developed and extends upward and forward to the walls of the braincase.
3. A distinct element connects the Squamosal with the Parietal bone above the Opisthotic.
4. The teeth have no roots.
5. There is no sacrum.
6. There is no sternum.
7. The limbs possess no condylar articular faces.

Von diesen sieben Merkmalen treffen wenigstens drei nicht zu:

Erstens kann man an unserem Material nicht bestätigen, dass das Squamosum (Opisthoticum) nach oben und hinten bis zu den Wänden der Gehirnkapsel reicht, da ohne Ausnahme beide Aeste, der obere und untere des Squamosum von der Gehirnkapsel ziemlich weit entfernt sind.

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[21] Bull. U. S. Geol. and Geogr. Surv. Territ. IV. 1878 p. 309

Zweitens, obwohl Prof. Marsh einen dritten Knochen im Quadratoparietalbogen gefunden haben will, der zwischen der nach oben und vorn gerichteten Spitze des Quadratojugale (Squamosum) und dem nach hinten gerichteten Processus des Parietale stände, ist es doch ganz sicher, dass wenigstens bei manchen unserer Exemplare von *Platecarpus*, die die Beziehungen der Knochen zu einander aufs Klarste zeigen, dieses nicht der Fall ist. So passen z. B. bei einem unserer Exemplare Squamosum (Opisthoticum), Quadratojugale (Squamosum) und der hintere Arm des Parietale—alle diese drei sind vollkommen erhalten—genau zusammen, wobei auf der Oberseite des Squamosum die Enden des Quadratojugale und Parietalarmes sich aneinander vorbeischieben, den ganzen Raum einnehmen und keinen Platz für einen dritten Knochen freilassen. Auch bei einem anderen Exemplar, an dem der Quadratoparietalbogen vollkommen ist und das die Theile im Zusammenhange zeigt, ist keine Sutur zu sehen, die auf einen überzähligen Knochen hinwiese.

Drittens, ein Sternum ist, wie Prof. Marsh[22] gezeigt hat, vorhanden, auch haben Williston and Case[23] Reste des Sternum mit den Costal Knorpeln gefunden, und in der Münchener Sammlung werden gleichfalls Reste des Sternum und der Costal Knorpel aufbewahrt.

Es ist auch der angegebene grosse Unterschied zwischen den nach unten gebogenen Seiten des Parietale eines Pythonomorphen und z. B. *Varanus bivittatus* schwer zu verstehen; bei beiden fangen etwas hinter den vorderen Ecken des Parietale zwei Lappen oder nach unten gebogene Ränder des Knochens an, die nach hinten bis zur Mittellänge etwas länger werden. Die vordere Seite ist schief abgeschnitten und hinter diesem schiefen Vorderrande legt sich der Lappen an den oberen nach vorn gerichteten Ast des Prooticum. Nur ist bei *Varanus* dieser Lappen oder nach unten gebogene Rand etwas kürzer als bei den Pythonomorphen.

Was die drei anderen Merkmale anbelangt, wie:

5. The teeth have no roots,
6. There is no sacrum,
7. The bones of the limbs have no condylar articular surfaces,

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[22] Americ. Jour. Science and Arts. Vol. XIX. Jan 1880 p. 83.

[23] Kansas Univ. Quart. Vol. I. July 1892 p. 15.

so scheint es zweifelhaft, ob sie wichtig genug sind, um Anlass zur Aufstellung einer neuen Ordnung zu geben.

Prof. OWEN hat die Meinung ausgesprochen, dass die Pythonomorphen unter den Lacertiliern die taxonomischen Aequivalente der Pinnipeden unter den Carnivoren sind[24] und in der letzten Zeit hat BAUR[25] folgende Classification vorgeschlagen:

Suborder: *Platynota*
Super-family: *Varanoidea*
Families: *Mosasauridae*, *Varanidae*
Super-family: *Helodermatidea*
Family: *Helodermatidae*

Ob nun die eine oder die andere Classification angenommen wird, soviel steht jedenfalls fest, dass die Pythonomorphen sehr grosse Verwandtschaft mit den Eidechsen haben und nicht genügend abweichende Merkmale besitzen, um ihre vollständige Trennung von denselben als selbständige Ordnung zu rechtfertigen.

TYLOSAURUS MARSH

Diese Gattung scheint nicht mit dem Genus *Liodon* OWEN übereinzustimmen, wie früher allgemein angenommen wurde. Sie weicht bedeutend im Character der Zähne von dem von OWEN beschriebenen Thiere ab. Die Zähne des *Liodon* waren, wie der Gattungsname besagt, glatt, während die des *Tylosaurus* wenigstens auf der Innenseite gestreift sind. Für den Fall, dass überhaupt das europäische Genus unter den bis jetzt in Amerika bekannten Gattungen vertreten war, müssten wir die Repräsentanten desselben bei der Gattung *Clidastes* suchen, da in ihm einige Species Zähne besitzen, die grosse Aehnlichkeit mit denen des OWEN'schen Genus zeigen.

Das Material im Münchener Museum, worauf sich die Beschreibung dieser Gattung stützt, enthält von *T. proriger*, Taf. III, einen sehr grossen Schädel, der sich durch Vollkommenheit und gute Erhaltung auszeichnet und sechs Halswirbel; es sind nur Theile des Ex-Occipitale und der Prootica verloren gegangen. Von einem zweiten Individuum liegen ein Theil des Schädels, Coracoideum, Scapula, Humerus, Ulna und 18 Wirbel und von einem dritten Individuum eine geschlossene Reihe von 25 Schwanzwirbeln vor.

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[24] I estimate the Mosasaurians in the Lacertilian order to be the equivalent to the Seals in the Ferine order. Quart. Jour. Geol. Soc. 1877 p. 715.

[25] Science XVI. Nov. 7. 1890 p. 262.

Von *T. dyspelor* wird ein fast completer Schädel, sowie die sehr schön erhaltene bis zum sechsten Schwanzwirbel vollständige Wirbelsäule aufbewahrt. *Tylosaurus micromus* ist durch zwei sehr schöne Schädel vertreten, von denen der eine (Taf. I Fig. 3) den ganzen oberen Theil des Kopfes, mit Ausnahme des hinteren Endes des Parietale, und den Unterkiefer im Zusammenhang zeigt; der zweite theilweise macerirte Schädel ist so vollkommen, dass nichts zu wünschen übrig bleibt. An beiden Skeleten sind auch die vordersten Wirbel vorhanden und zwar 6 Halswirbel beim ersten und sieben Hals- und die drei ersten Rückenwirbel bei dem zweiten. Zu den genannten Resten kommen noch eine Wirbelsäule (wahrscheinlich *T. micromus*) mit dem grössten Theil des Schwanzes, den hinteren Rückenwirbeln, dem vollständigen Beckengürtel und von den Hinterextremitäten Femur, Tibia und Fibula. Von einem anderen Individuum (*T. proriger*) liegen ein sehr grosser Humerus mit Radius und Ulna vor.

Die Wirbelsäule

von *Tylosaurus* war, wie bei allen Pythonomorphen in Hals-, Rumpf- und Schwanzabschnitt getheilt. Von den nahezu 118 Wirbel kommen auf den Hals sieben, den Rücken 23 und den Schwanz ca. 88. Die beiden Seitenstücke des Atlas waren, von der Seite gesehen, viereckig mit verticalem Vorder- und Hinterrand und schräg nach hinten und oben abgestutztem Unterrand. Vom vorderen Theil des Oberrandes ging jederseits ein abgeplatteter Fortsatz aus, der sich über das Rückenmark bog und wahrscheinlich mit dem zweiten Seitenstück der anderen Seite durch ein Band verbunden war, wie bei den Eidechsen. Der Hinterrand besass keinen langen nach hinten und unten gerichteten Fortsatz, wie bei *Clidastes*, sondern war meistens an Stelle dieses Fortsatzes nur mit einem kleinen Ohr versehen. Die Hypapophyse des Atlas war gross, unten mässig lang ausgezogen und reichte nach hinten bis zur Hypapophyse des Epistropheus. Sie war an ihrem hinteren Ende, wo sie an die Apophyse des Epistropheus anstiess, abgestutzt, was allein nur bei *Tylosaurus* vorzukommen scheint. Der Epistropheus besass einen niederen, breiten nach hinten gerichteten Dornfortsatz, der hinten stärker und mit zwei Zygapophysen versehen war. Die Ansatzstelle für die Hypapophyse war gewöhnlich etwas viereckig und pyramidal vertieft; der Dornfortsatz des dritten Halswirbels war etwas dünner als der des zweiten und stand fast vertical. Die Zygapophysen waren gross, erreichten jedoch nicht die Dimensionen derer des dritten Wirbels von *Platecarpus*. Der Gelenkkopf war rundlich, ebenso der des Epistropheus. Am siebenten Wirbel ist der Dornfortsatz breiter und dünner geworden und vorn und hinten zugeschärft, die Zygapophysen sind kleiner und die länger gewordene Hypapophyse besitzt nur eine minimale Ansatzstelle für das Endstück, das möglicherweise nur aus Knorpel bestand. Bei dem 8. Wirbel (ersten Rückenwirbel), sowie beim 9. und 10. ist die Hypapophyse auf einen kleinen Höcker reducirt. Am 10. Wirbel ist der untere Theil der S-förmig gebogenen Diapophyse, die beim 7. und auch bis zu einem gewissen Grad beim 9. horizontal nach vorn bis zum Rande der Aushöhlung des Centrums verläuft, fast verschwunden und existirt nur als kleine Leiste an der vorderen unteren Ecke der Diapophyse; desgleichen sind an demselben 10. Wirbel die Diapophysen länger als die des letzten Halswirbels, auch sind sie schmäler und oft etwas nach oben gerichtet. Die Zygapophysen bleiben ziemlich stark, das Zygosphen ist jedoch verschwindend klein. Der Dornfortsatz ist breit und der Gelenkkopf bald horizontal (*Tyl. proriger*) bald vertical (*Tyl. dyspelor*) zusammengedrückt. Bis zum 11. Rückenwirbel bleiben die Wirbel dem 3. ziemlich gleich, während die Zygapophysen langsam schwächer werden. Mit dem 11. Rückenwirbel tritt jedoch eine Aenderung ein, indem die Diapophysen kürzer werden und etwas nach unten rücken, bis sie schliesslich von der Mittelhöhe der Seite des Centrums ausgehen; die Zygapophysen verschwinden nach und nach und die Gelenkköpfe fangen an, die pentagonale Gestalt anzunehmen, die bei den hinteren Rückenwirbeln und Schwanzwirbeln so ausgesprochen ist. Beim 20. Wirbel sind die Zygapophysen fast spurlos verschwunden, die Diapophysen kurz und auf den unteren Theil der Seite des Centrums heruntergerückt, ferner ist die eckige Gestalt des Gelenkkopfes stark ausgeprägt. Beim 23. Wirbel (letzten Rückenwirbel) ist die Diapophyse noch etwas kürzer. Die Neurapophysen bleiben bis zum Ende des Rückens breit und hoch.

Die Pygialwirbel hatten lange dünne Diapophysen und stark eckige Gelenkköpfe, auch waren die Unterseiten der Centren zwischen den Diapophysen in drei Facetten getheilt.

Hinter den Pygialwirbeln besitzen die Schwanzwirbel bis zur Mitte des Schwanzes kurze Diapophysen, die allmählich in die Mittelhöhe des Centrums heraufrücken, wo sie schliesslich verschwinden. Bis zu der Stelle, wo die Diapophysen verschwinden sind die Chevron tragenden Wirbel ähnlich denen des Pygialabschnittes, auf der Unterseite mit drei Facetten versehen, von denen die zwei seitlichen mit den Diapophysen nach hinten heraufrücken und sich abrunden, bis die eckige Gestalt des Gelenkkopfes sich zu einer ausgezeichnet vertical-elliptischen Gestalt verändert hat. Hinter dem Pygialabschnitt tragen die Schwanzwirbel Chevron-Bones, die mit den Centren gelenkig verbunden sind.

Bei *Tylosaurus* scheinen, wie bei den anderen Gattungen, die Rippen mit dem zweiten Halswirbel angefangen und sich bis zum ersten Beckenwirbel fortgesetzt zu haben.

Die Extremitäten

Im Schultergürtel war die Scapula sehr klein im Verhältniss zur Grösse des Coracoideum. Letzteres war scheibenförmig, dick und mit einem Foramen in der Nähe des proximalen Ende versehen. Der Humerus war verflacht, wie bei den anderen Gattungen, in der Mitte verjüngt und fast gleich breit an den beiden Enden. Am proximalen Ende war eine grosse Crista vorhanden. Radius und Ulna, die ungefähr $\frac{3}{4}$ so lang waren wie der Humerus, waren in der Mitte verjüngt und an den Enden etwas verdickt; der Radius war am distalen, die Ulna am proximalen Ende am breitesten.

Der Beckengürtel war durchaus eidechsenartig. Das lange, schlanke Ilium war wahrscheinlich mit den Diapophysen des ersten Pygialwirbels durch Knorpelbänder verbunden. Das Pubis, welches dem Darmbein sehr ähnlich sieht, war nicht ganz so lang, wie letzteres und zeigte gewöhnlich Andeutungen eines Foramens am proximalen Ende. Das Sitzbein war wie bei den Schildkröten und manchen Eidechsen ausgebreitet, wobei gleich unter dem Kopf des Knochens die Erweiterung anfängt und der Hinterrand etwas concav ist. Das Femur war etwas schlanker als der Humerus und zeigte eine grosse, am schmalen, proximalen Ende gelegene Crista. Tibia und Fibula waren ungleich gross, die Tibia zweimal so breit wie die Fibula. Die Carpalien, Tarsalien und Phalangen in unserer Sammlung zeigen keine Differenzen von denen anderer und besser bekannter Gattungen.

Der Schädel

Das Basioccipitale (Taf. IV Fig. 1) von *Tylosaurus*, das mit dem von *Varanus* sehr viel Aehnlichkeit hat, bildete mit Ausnahme von zwei kleinen Ecken oben rechts und links, die von dem Ex-Occipitale zusammengesetzt wurden, den ganzen Gelenkkopf. Vorn lief es in zwei sehr breite Fortsätze (Hypapophysen) aus, die am Unterende eine lanzettförmigen Muskelansatzstelle besassen. Die Muskelansatzstelle scheint immer hinten breiter gewesen zu sein, im Gegensatz zu der anderer Gattungen, bei denen sie entweder keine bestimmte Gestalt hatte oder rundlich war. Dass die Hypapophysen auf der Vorderseite dünner werden, wurde dadurch veranlasst, dass die beiden nach hinten gerichteten Fortsätze des Basisphenoids, anstatt gegen die Hypapophysen zu stossen und dort aufzuhören, sich an der Innenseite der Hypapophysen vorbeischoben und fast den Hinterrand erreichten. Oft sind die Ansatzzellen dort, wo sie sich an die Innenseite der Hypapophysen anlegen, tief und rauh. Der seitliche Fortsatz des Ex-Occipitale, der sich bei *Platecarpus* über die hintere Hälfte der Oberseite der Hypapophyse hinaus erstreckt und dieselbe bedeckt, war bei *Tylosaurus* klein und bedeckte nur ein ganz kleines dreieckiges Feld am proximalen Ende der hinteren Hälfte der Apophyse.

Die Ex-Occipitalia, die, wie oben erwähnt, geringen Antheil an der Bildung des Gelenkkopfes hatten, bildeten die Seiten des Foramen magnum und schickten nach hinten zwei lange Arme aus, die auch zum Theil aus den mit den Occipitalia lateralia verschmolzenen Opisthotica bestanden. Die Arme waren am hinteren Ende dünn, horizontal zusammengedrückt und auf ihrer ganzen Aussenseite vom Prooticum und Squamosum bedeckt, die in ungefähr der Mittellänge des Armes zusammenstiessen.

Das Occipitale superius sitzt auf den Ex-Occipitalia und der Hinterseite der vorderen heraufsteigenden Aeste der Prootica und ist mit ihnen so eng verbunden, dass die Suturlinien oft sehr undeutlich sind. Es ist hinten etwas dachförmig; die beiden Seiten gehen vom Hinterende aus nach vorn etwas auseinander, entsprechend den hinten verwachsenen, vorn auseinandergehenden und herunterhängenden Lappen des Parietale. Es bildete den obersten Theil des Foramen magnum und nahm am Oberrand die verwachsenen Lappen des Parietale in einer Einkerbung auf.

Das Basisphenoid, Taf. IV Fig. 4, hat von unten gesehen, einige Aehnlichkeit mit dem Buchstaben *x*, wobei jedoch ein fünfter sehr kleiner Ast, das Rudiment des Parasphenoids vom Centrum nach vorn und oben ausgeht. Es stiess in einer ebenen Verbindungsfläche mit dem Basioccipitale zusammen und stand ausserdem mit diesem durch zwei divergirende, nach hinten gerichtete Fortsätze in Verbindung, die sich an dem dünnen Vorderende der flachen Hypapophysen des Basioccipitale vorbeischoben und hauptsächlich auf der Innenseite derselben lagen. Vom Vorderende des Basisphenoid geht rechts und links je ein in verticaler Richtung comprimirter Fortsatz aus, der schräg von vorn nach hinten und aussen abgestutzt war und ursprünglich mit dem Pterygoid durch Ligament verbunden war. Diese Processi sind bei *Tylosaurus* kaum halb so lang wie die hinteren, im Gegensatz zu *Platecarpus*, bei dem die vorderen und hinteren ungefähr dieselbe Länge haben. Der oben erwähnte Rest des Parasphenoid (Praesphenoid) geht zwischen den beiden vorderen Aesten des Basisphenoids nach vorn und oben aus und zeigt gewöhnlich eine lange, sehr schlanke Gestalt.

Die Seitenwände der Gehirnhöhle werden zum grossen Theil von den Prootica gebildet, die unten auf dem Basisphenoid und Basioccipitale liegen und hinten mit den Ex-Occipitalia und oben mit Occipitale superius und Parietale zusammenstossen. Sie erhielten dadurch eine etwas dreiästige Gestalt, dass der Vorderrand wie bei *Varanus* tief ausgeschnitten war und die Hinterseite in einen langen Arm, der sich auf die Aussenseite des Armes des Ex-Occipitale erstreckte, ausgezogen war. Der obere der zwei vorderen Aeste war meistens ziemlich dünn und lang und trug einen grossen Theil der Parietallappen. Der untere Ast legte sich an das Basisphenoid und Basioccipitale, während der hintere Ast, wie oben erwähnt, sich hinaus auf den Arm des Ex-Occipitale bis zur Mittellänge desselben erstreckte und da an das Vorderende des Unterastes des Squamosum stiess. An der Basis des hinteren Armes stossen der vordere Theil des Ex-Occipitale und der hintere Theil des Prooticums zusammen. Das Occipitale superius sitzt auf der Oberseite des Prooticums zwischen dem hinteren und dem obersten der vorderen Aeste auf und ist mit dem Prooticum durch eine sehr verwickelte Sutur verbunden.

Das Parietale, Taf. IV Fig. 7, ist bei *Tylosaurus* von sehr characteristischer Gestalt und unterscheidet sich durch seine ebene obere Fläche von dem des *Platecarpus*, das immer am vorderen Theil der Oberseite etwas über das Niveau des hinteren Theiles erhoben ist. Es war lang, vorn breit und nach hinten allmählich verjüngt, oben ganz flach ohne ein erhabenes Feld und lief an den Seiten in scharfe Ränder aus. Das Foramen parietale war klein und lag auf der Grenze zwischen Parietale und Frontale. An der rechten und linken Ecke des Vorderrandes kommt das Scheitelbein in Berührung mit dem Postfrontoorbitale und an beiden Seiten hinter diesen Ecken fängt auf der Unterseite ein herunterhängender Lappen an, der sich nach hinten streckt und mit dem von der andern Seite im hinteren Drittheil des Parietale verwächst. Die Lappen sind am Vorderende schräg abgestutzt und hinter dem Punkt, wo sie verwachsen, nach hinten rechteckig ausgeschnitten, so dass der Unterrand des verwachsenen Theiles viel höher steht. Die mittleren freien Theile, die am weitesten herunterreichen, legen sich an die oberen, nach vorn gerichteten Aeste der Prootica; die verwachsene Partie passt in eine Einkerbung am Oberrand des Occipitale superius.

Das Squamosum, Taf. II *Sq.*, (Opisthoticum Cope) ist ein zweiästiger Knochen, der das Suspensorium für das Quadratum bildet. Der untere Ast liegt auf der Aussenseite der hinteren Hälfte des nach hinten gerichteten Armes des Ex-Occipitale, stösst ungefähr in der halben Länge desselben an den entgegenkommenden Arm des Prooticum und schiebt sich eine Strecke weit zwischen denselben und das Ex-Occipitale. Die oberen Aeste, die die untere Partie des Quadratoparietalbogens zusammensetzen, richten sich nach oben und innen, sind ziemlich breit und dünn und nicht ganz so lang, wie die unteren. Zur Aufnahme des Quadratumkopfes wird das Hinterende des Squamosum nach aussen gebogen und die Aussenseite gleich vor dieser Biegung etwas ausgehöhlt und dadurch die innere, hintere und ein Theil der Oberseite der Gelenkpfanne gebildet.

Das Frontale, das von dem aller anderen Gattungen durch die Verzierung auf seiner Oberseite, nämlich durch längliche, vom Parietalloch nach vorn ausstrahlende Gruben zu unterscheiden ist, war dreieckig, über den Augenhöhlen nicht ausgeschnitten und hinten eher etwas convex als herzförmig eingeschnitten, wie bei

Platecarpus. Vorne war es in zwei Spitzen (Hauptspitzen) getheilt, die die vorderen Enden der verschmolzenen Frontalia darstellen. Das Frontale bei *Tylosaurus* war von der Begrenzung der Augenhöhlen durch das Uebergreifen des Postfrontale über das Hinterende des Praefrontale ausgeschlossen. Am vorderen Ende des Contactes mit dem Praefrontale war der Seitenrand des Frontale etwas eingebuchtet, wodurch auf jeder Seite eine vorragende Spitze (Nebenspitze) gebildet wurde, während die Einbuchtung das Hinterende des Nasenloches darstellt.

Die Postfrontoorbitalia, Taf. I Fig. 3 *Ptf.*, Taf. II *Ptf.*, bedecken die Unterseite der hinteren Ecken des Frontale und legen ihre Spitzen vor deren Enden in Vertiefungen auf der Aussenseite der Praefrontalia, auf der sie sich nach vorn bis zu einem Punkt über dem vordersten Rand der Augenhöhle erstrecken und dadurch das Frontale von jedem Antheil an der Begrenzung der Augenhohlen ausschliessen. Die Postfrontoorbitalia stehen in Verbindung mit dem Quadratojugale und Jugale, welche Knochen einander gewöhnlich auf ihrer Unterseite berühren und infolgedessen den oberen Theil des Jochbogens und den vorderen Theil des Schläfenbogens bilden. Sie sind mit dem Jugale durch einen kurzen abgerundeten und nach unten gerichteten Fortsatz verbunden und mit dem Quadratojugale durch einen langen Stiel, der sich mit einem sehr ähnlichen Fortsatz des Quadratojugale durch eine complicirte Sutur verbindet.

Das Quadratojugale, Taf. II *Qu. J.*, Taf. IV. Fig. 6, früher für das Squamosum gehalten, beweist seinen quadratojugalen Character dadurch, dass es, wie oben gesagt, am Vorderende mit dem Jugale in Berührung tritt. Bei den lebenden Eidechsen verhalten sich diese beiden Knochen zu einander sehr verschieden, bei einigen berühren sie sich gar nicht, bei anderen sind sie fest verbunden. Hinten legt es sich mit breitem Kopf an die Aussenseite des Oberastes des Squamosum und bildet den oberen Theil der Gelenkpfanne des Quadratum. Dieser Kopf ist für unsere Gattung dadurch characteristisch, dass er hinten etwas nach unten gebogen ist und sich am Oberrand als ein länglicher Flügel ausbreitet, der bei den anderen Gattungen in der Längsrichtung meist sehr kurz ist und am Oberrand sich etwas zuspitzt.

Das Quadratum, Taf. II *Qu.*, Taf. III Fig. 1, 2, war frei beweglich in der vom Squamosum und Quadratojugale gebildeten

Gelenkpfanne. Die Vorderseite verbreitet sich nach aussen zu einem breiten, hinten concaven, vorn etwas convexen Flügel, dessen mittlerer, dünner Theil gewöhnlich weggebrochen ist. Vom Oberende geht ein kräftiger Supracolumellar-Fortsatz aus, der kurz und am Ende spitzig ist. Unter dem Meatus auditorius steht ein leistenartiger Vorsprung, der zusammen mit dem Supracolumellar-Fortsatz den Meatus zu Dreiviertel umschliesst. Der Oberrand der Vorderseite war tief, der der Innenseite wenig eingebuchtet und die vordere innere Ecke oben ziemlich spitz. Diese sämmtlichen Merkmale könnten als Unterschiede von den anderen Genera benutzt werden. Die Stapedialgrube ist meistens länglich und in der Mitte etwas eingeengt. Der Stapes war lang und schlank, wie bei *Platecarpus* und an den Enden etwas angeschwollen.

Das Praefrontale, Taf. I *Prf.*, Taf. III Fig. 8, Taf. I Fig. 3 *Prf.*, scheint bei den Pythonomorphen ein sehr veränderliches Element gewesen zu sein und besitzt bei jeder von den drei Gattungen *Platecarpus*, *Clidastes* und *Tylosaurus* eine ziemlich bestimmte Form, die von jener der anderen Genera bedeutend abweicht. Bei *Tylosaurus* ist es dreieckig, wobei der Hinterrand von den Augenhöhlen bogenförmig ausgeschnitten wird und der Ober- und Unterrand fast gerade bleiben. Der Oberrand stand mit dem Frontale vom hinteren Fünftel desselben bis zu den Nebenspitzen in Berührung und war entlang des Contactes horizontal rautenförmig ausgebreitet. Auf der Aussenseite des Hinterendes liegt unmittelbar unter dem Oberrand eine längliche Vertiefung, in welche sich das Vorderende des Postfrontale einfügte. Die Aussenseite war infolge eines zungenförmigen Ausschnittes am Hinterende des Oberflügels des Maxillare zum grossen Theil unbedeckt, während das Vorderende sich an die Innenseite des Flügels anlegte und nach vorn bis über den 7. Maxillar-Zahn reichte. Der Hinterrand war etwas nach innen eingeschlagen und meistens unten stumpf abgeschnitten, anstatt scharf zu endigen wie bei *Platecarpus*.

Das Vorhandensein eines Superciliare bei *Tylosaurus* ist bis jetzt nicht constatirt worden.

Das für dieses Genus durchaus characteristische Praemaxillare, Taf. II *Pmx.*, Taf. I Fig. 3 *Pmx.*, war vorn schnabelartig verlängert, rundlich im Querschnitt und am Ende stumpf abgeschnitten. Die schnabelartige Verlängerung war nicht ganz so lang wie der bezahnte Theil des Praemaxillare und zeigte auf seiner Unterseite vor dem ersten Paar Zähne einen kleinen Wulst. Nach hinten verlängerte sich der Zwischenkiefer in einen langen Stiel, der hinten mit den Nasalia verschmolz und sich an das Vorderende des Frontale anlegte. Der Stiel war bis zum 6. Maxillar-Zahn von den beiden Maxillen eingefasst und fast gleichmässig breit, er verjüngte sich dann plötzlich und wurde hinten, wo er auf dem Frontale lag, wieder etwas breiter. Der bezahnte Theil zeigt auf jeder Seite zwei kräftige, gekrümmte Zähne, die fein gestreift und schwach facettirt sind und vorn und hinten eine schwache Kante besitzen. Hinter dem letzten Zahnpaar und unter dem Stiel stehen zwei plattenartige, horizontal comprimirte, nach hinten gerichtete Fortsätze, die von den Maxillen eingefasst werden und zwischen sich die Spitzen der vorderen Enden der Vomera aufnehmen.

Die Nasalia waren, wie vorhin bemerkt, mit dem Stiel des Zwischenkiefers verschmolzen, bedeckten mit demselben das Vorderende des Frontale und begrenzten einen Theil der Innenseite der Nasenlöcher.

Die Maxillen, Taf. II *Max.*, Taf. I Fig. 3 *Max.*, hielten, bezüglich ihrer Länge, zwischen denen von *Clidastes* und *Platecarpus* die Mitte, waren vorn mit dem Praemaxillare bis zum 6. Zahn durch Sutur verbunden und infolge dessen oben bis zu diesem Punkt nach hinten schief abgeschnitten. Der Oberrand war ganz wenig concav hinter der Sutur zwischen Maxillare und Praemaxillare, im Gegensatz zu *Platecarpus*, bei dem er ziemlich tief ausgeschnitten ist. Auf dem Innenrand des bezahnten Theiles stand das Palatinum zwischen dem 9. und 13. Zahn mit dem Maxillare in Berührung, während vom Vorderende bis zum 4. Zahn die Maxillen zwischen sich die Vomera und die beiden Fortsätze des Zwischenkiefers einfassten. Am hinteren Ende legte sich das Vorderende des Jugale an, auch kam das Maxillare mit der Vorderspitze des Transversum in Berührung. Die Oberkiefer waren mit 13 starken Zähnen besetzt, Taf. II, die im Wesentlichen denen des Zwischenkiefers ähnlich waren.

Die fast genau wie bei den Eidechsen beschaffenen Vomera, Taf. I Fig. 3 *V.*, stiessen wie bei diesen vorn zusammen und waren von zwei, vom bezahnten Theil des Praemaxillare nach hinten vorspringenden Fortsätzen und hinter diesen von den Maxillen umfasst, divergirten aber von dem Punkt, wo sie nicht mehr mit den Maxillen in Berührung standen, nach hinten und stiessen an ihren

Hinterenden mit den Palatinen zusammen. Der vordere Theil des Vomers, der mit dem Praemaxillare und Maxillare in Contact stand, war auf der Aussenseite etwas angeschwollen und könnte als Kopf bezeichnet werden. Die Aussenseite des Kopfes war punktirt, wie die Fläche des Maxillare, an die sie sich anlegte; diese Punktirung scheint auf *Tylosaurus* beschränkt zu sein. Die Hinterenden der Vomera, wo sie mit den langen vorderen Processi der Palatina zusammenstossen, sind auf der Innenseite von oben tief gespalten; diese Spalten nehmen die Palatinen auf. Da aber der Haupttheil des Vomers auf der Aussenseite des Spaltes liegt und auch am weitesten heraufreicht, so könnte es scheinen, als ob die Palatinenstiele sich einfach an der Innenseite der Hinterenden der Vomera vorbeischöben.

Turbinalia, Taf. I Fig. 3 *Turb.* Bei einem Exemplar von *Tylosaurus*, das alle Knochen des Schädels, mit Ausnahme des oberen Theiles des Hinterhauptes und hinteren Theiles des Parietale vollkommen erhalten und im Zusammenhang zeigt, liegen zwischen dem Zwischenkieferstiel und der oberen Parthie der Maxillen zwei Bildungen, die unzweifelhaft die Turbinalia darstellen. Von oben gesehen bedecken sie das vordere Drittheil der Nasenlöcher, indem sie als dünne mantelartige Knochen mit dem einen Rand auf den fast verticalen Seiten des Praemaxillen-Stieles und mit dem anderen auf den Maxillen über den Vomern stehen und so die Nasenlöcher vollkommen überbrücken. Vorn kann man sie von der Unterseite bis zum 3. Maxillar-Zahn verfolgen, wo sie unten vom Vomer, oben vom Zwischenkieferstiel verdeckt werden. Nach hinten erstrecken sie sich bis zum 7. Zahn und sind hier abgebrochen, ursprünglich haben sie jedoch wohl eine kurze Strecke weiter gereicht. Die bei diesen Knochen sehr dichte und spröde Knochensubstanz hat sehr viel Aehnlichkeit mit der der Augenplatten. Dass hier die Turbinalia vorliegen, scheint ausser Zweifel, da am Schädel keine anderen derartigen Bildungen vorkommen und sie genau an der Stelle liegen, wo man die Turbinalia erwarten würde.

Das Palatinum, Taf. I Fig. 3 *Pl.*, das wie bei den Lacertiliern mit Maxillare, Vomer, Praefrontale und Pterygoid in Verbindung stand, war ein unregelmässig viereckiger Knochen mit einem, vom Vorderende des Innenrandes nach vorn auslaufenden, stielartigen Fortsatz, der in die Spalte am Hinterende des Vomer aufgenommen wurde. Der Aussenrand des viereckigen Haupttheiles war mit einer breiten, tiefen Längsrinne versehen, die den Innenrand des bezahnten Theiles der Maxilla vom 9. bis zum 13. Zahn aufnahm. Die etwas ausgehöhlte Oberseite besass einen dünnen aufsteigenden Innenrand und erhob sich hinten in einen dicken, im horizontalen Querschnitt oft dreieckigen Fortsatz, der am Oberende entweder etwas zugeschärft oder stumpf abgeschnitten sein konnte und auf welchem die hintere Parthie des Praefrontale sass.

Das Pterygoideum, Taf. IV Fig. 5, ist bei *Tylosaurus* besonders gross und plump und legt sich mit seinem dünnen Vorderende an die Unterseite des keilförmig auslaufenden Hinterendes des Palatinum, hinten ist es wie bei den Varaniden mit dem distalen Ende des Quadratum verbunden. Der bezahnte Theil ist sehr wenig S-förmig gebogen und mit 10 bis 11 etwas pleurodonten Zähnen besetzt, die kürzer und stärker gekrümmt sind, als die der Kiefer. Die Pterygoidzähne waren im Querschnitt fast rund und hatten zwei sehr schwache Kanten, die das vordere Drittheil begrenzten. Die Zahl scheint nicht ganz constant zu sein, da an einem der schönsten Exemplare das eine Pterygoid 10, das andere 11 Zähne trägt. Der bezahnte Theil lief hinten in eine scharfe Spitze aus; er schickte von einer Ausbreitung der Aussenseite zwischen dem 11. und 5. Zahn einen Transversal-Processus nach der Seite aus, der mit dem Transversum verbunden war. Der unbezahnte hintere Theil, der mit dem Quadratum in Verbindung steht, zeigt am hinteren Ende einen etwas gebogenen Kopf, der dem Genus *Tylosaurus* eigenthümlich ist.

Columella. Bei dem vollkommen erhaltenen Schädel von *Tylosaurus micromus* liegt auf jeder Seite des Basisphenoids ein kleiner Knochen, der mit seinem Unterende das Flügelbein an der Stelle berührt, auf der bei *Varanus* die Columella aufsitzt, und sich nach oben bis auf den unteren vorderen Ast des Prooticum erstreckt, wo er abgebrochen ist. Da die Flügelbeine, mit Ausnahme davon, dass sie von den Seiten her zusammengepresst sind, bis sie einander berühren, in ihrer natürlichen Lage blieben, so scheint es unmöglich, dass die zwei Knochen Zungenbeine sein können, weil diese durch einen seitlichen Druck nicht so hoch hinaufgeschoben werden könnten und sonst unter oder zwischen den Pterygoiden liegen müssten. Da die beiden Knochen genau die richtige Lage haben, darf man annehmen, sie seien die Columellae.

Das Transversum, Taf. IV Fig. 3, 5, das bei einem der Schädel ganz vollständig und im Zusammenhang mit dem Pterygoid erhalten ist, zeigt zwei Aeste, die fast senkrecht aufeinander stehen und den Transversal-Processus des Pterygoid mit dem Jugale und dem Hinterende des Maxillare verbinden. Der innere Ast ist dünn, sehr breit und am Innenende durch einen tiefen Einschnitt in zwei Spitzen getheilt, von denen die vordere am längsten ist. Die Oberseite des Innenendes besteht aus zwei Flächen, die unter einem stumpfen Winkel zusammenstossen und durch eine Linie getrennt sind, die von der Vorderseite der vorderen längeren Spitze des Innenendes schräg hinüber zur hinteren, äusseren Ecke des Transversum verläuft. Die hintere Fläche war rauh und legte sich an die untere entsprechend sculptirte Seite des Transversalprocessus des Pterygoids. Der äussere Ast steht parallel der Längsachse des Kopfes, ist schmal und schwach, und mit einer Ausnahme, an allen Exemplaren weggebrochen. Er fügt sich in eine Vertiefung ein, die hinter derjenigen für das Maxillare auf der Innenseite des unteren Astes des Jugale liegt, und reicht nach vorn bis zum Maxillare, dessen Hinterende er berührt.

Das wie bei allen Pythonomorphen gut entwickelte Jugale, Taf. II *Jug.*, war, wie oben erwähnt, mit dem Postfrontoorbitale verbunden und berührte das Vorderende des Quadratojugale. Vom Postfrontoorbitale läuft es eine kurze Strecke senkrecht hinunter, biegt dann knieförmig um und erstreckt sich nach vorn zum Hinterende des Maxillare, auf dessen Aussenseite es sich anlegt. Auf der Innenseite des unteren Astes sind zwei rinnenartige Vertiefungen vorhanden, die eine vorn, in die das Hinterende der Maxillare einpasst, die zweite, in die sich der Aussenast des Transversum einfügt, unmittelbar hinter der ersten und bis fast zur Umbiegung verlaufend.

Das Lacrymale erscheint bei *Tylosaurus* als eine meistens formlose Masse auf dem Hinterende der Maxillare, zwischen Maxillare und Praefrontale. Es unterscheidet sich durch seine rauhe Oberfläche von den anderen benachbarten Knochen.

Die Mandibeln, Taf. II, waren lang und schlank und in der Symphyse durch Ligament verbunden. Sie bestanden je aus zwei Theilen, einem vorderen, der vom Dentale und Operculare zusammengesetzt war und einem hinteren, der vom Articulare, Angulare, Supraangulare und Coronoideum gebildet wurde. Sie waren halbgelenkig mit einander verbunden und konnten wahrscheinlich gegeneinander etwas gebogen werden, wodurch das Vergrössern des Rachens und das Schlucken grösserer Beutestücke ermöglicht wurde.

Das vorn fast gerade abgestutzte Dentale war eine kurze Strecke weit unbezahnt. An der oberen Ecke des hinteren Endes trat das Dentale mit dem hinteren Theil des Mandibel dadurch in Verbindung, dass es an den vertical abgeschnittenen Theil des zugeschärften Vorderendes des Supraangulare stiess und das Coronoideum etwas herüber auf das Dentale griff. Das Zahnbein besitzt, wie das Maxillare, 13 starke Zähne, die vorn und hinten eine schwache Kante besitzen, innen stark gestreift sind und aussen eine schwache Streifung, sowie Andeutungen von Facettirung zeigen. Auf der Innenseite der unteren Hälfte des Dentale lag das Operculare, das nach hinten und unten etwas über das Hinterende des Dentale herüberragte und nach vorn bis zum vorderen Drittheil des letzteren reichte. Es war hinten zu einem breiten Kopf angeschwollen, dessen Hinterseite ausgehöhlt war und zur Aufnahme des entsprechend abgerundeten Kopfes des Angulare diente. Vor dem Kopf bestand es der Hauptsache nach aus zwei vom Unterrand heraufsteigenden Knochenlamellen, die zwischen sich die vordere Parthie des langen dünnen Vordertheiles des Articulare aufnahmen. Am hinteren Theil des Unterkiefers bildeten Articulare und Supraangulare die Gelenkpfanne zur Aufnahme des Quadratum. Jedes bildete die Hälfte der Pfanne; sie wurden durch eine von vorn schief nach hinten und aussen verlaufende Linie getrennt. Das Articulare bildete den kurzen, abgerundeten Theil des Kiefers hinter der Gelenkpfanne, setzte die innere hintere Hälfte derselben zusammen und dehnte sich dann entlang der Innenseite des Supraangulare bis zum Operculare aus, wo es, wie oben erwähnt, von den beiden Lamellen des Operculare aufgenommen wurde. Das Supraangulare, das den grössten Theil der Aussenseite des hinteren Theiles des Unterkiefers bildete, wurde vorn vom Dentale, unten vom Angulare, hinten und zum Theil auf der Innenseite vom Articulare begrenzt, während es auf dem Vorderende des Oberrandes das Coronoideum ritt. Im Gegensatz zu *Clidastes*, bei welchem das Coronoideum sehr lang ist, hatte die ziemlich dicke Parthie des Oberrandes zwischen der Gelenkpfanne des Quadratums und dem Coronoideum ungefähr die Länge des letzteren. Das Angulare war am Vorderende, wie das Operculare, zu einem dicken Kopf angeschwollen und fügte sich in die Aushöhlung am hinteren Ende des Kopfes des Operculare. Die Oberseite des Angulare was ausgehöhlt und umfasste mit seinen Seitenrändern den Untertheil des Supraangulare und Articulare. Das Coronoideum, das demjenigen von *Varanus* sehr ähnlich ist, sass auf dem Oberrand des Supraangulare, ragte mit seinem Vorderende über das des Supraangulare vor und legte sich an das hintere Ende des Dentale. Das hintere Ende war etwas flügelartig verbreitert und ragte etwas herauf, jedoch nicht so hoch, wie bei *Clidastes.*

Das Zungenbein, Taf. I Fig. 3 *Hy.*, welches von Prof. MARSH entdeckt wurde,[26] ist ein etwas gebogener Stab, der am einen Ende schief abgeschnitten ist und am anderen Ende etwas breiter wird. Es fehlt keinem Exemplare der Münchener Sammlung.

Das Material des Münchener Museums gestattet drei Species zu unterscheiden, nämlich: *T. dyspelor* COPE, *T. micromus* MARSH und *T. proriger* COPE. *T. dyspelor*, von welchem ein fast vollständiger Schädel und die geschlossene Wirbelsäule bis zum 6. Schwanzwirbel vorhanden sind, weist aufs Klarste die Merkmale dieser Species auf. Die Halswirbel sind im Allgemeinen quer-elliptisch, jedoch ist der dritte ebenso hoch wie breit und der vierte vertical-elliptisch. Die Rückenwirbel sind vertical zusammengedrückt. Der Schädel zeichnet sich besonders aus: 1) durch die Mandibeln, die am Vorderende nicht gerade gestutzt, sondern abgerundet und schmal sind; 2) durch das Basioccipitale, dessen Hypapophysen, obwohl sie ausgesprochen *Tylosaurus*-artig sind, seitlich nicht so stark zusammengedrückt und parallel der Längsachse des Kopfes kaum als halb so breit sind, wie bei *T. proriger* und *T. micromus*, 3) durch die Pterygoidea, die ihren Transversal-Fortsatz in der Nähe des 6. Zahns hinaussenden, und 4) durch die Kieferzähne, die rundlicher sind und auf der Aussenseite fast gar keine Facetten und keine Streifung zeigen, während die Innenseite eine starke Streifung aufweist.

T. proriger, Taf. II, ist durch einen wundervoll erhalten Schädel, welchem nur das Ex-Occipitale, Occipitale superius und das rechte Prooticum fehlen, vertreten. Von der Wirbelsäule dieses Individuums sind leider nur Halswirbel vorhanden, aber von einem zweiten liegen ausser den Schädelknochen und Extremitäten, Hals- und Rückenwirbel vor. Die Halswirbel sind meistens wie bei *T.*

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[26] Amer. Journ. Science. Vol. XIX. Jan. 1880, p. 84.

dyspelor eher transversal- als vertical-elliptisch; einige haben aber eine ausgesprochen vertical-elliptische Gestalt. Die Gelenkköpfe der Rückenwirbel sind wie bei *T. dyspelor* horizontal-elliptisch. Das Basioccipitale unterscheidet sich erheblich von dem des *T. dyspelor* durch die dünnen, in der Richtung der Längsachse des Knochens sehr breiten Hypapophysen und durch den niederen Grad von Einkerbung der Oberseite durch das Foramen magnum. Die Pterygoidea scheinen den Transversalprocessus immer von einem Punkt, nahe dem 8. Zahne, auszusenden. Die Mandibeln sind vorn sehr breit, gerade abgestutzt und besitzen wie die Maxillen und Zwischenkiefer Zähne, die etwas stärker facettirt sind als bei *T. dyspelor.* Das Articulare biegt sich hinter der Gelenkpfanne sehr wenig nach unten. Ich habe es nach der Beschreibung von Cope sehr schwierig gefunden, die Species *T. dyspelor* und *T. proriger* auseinander zu halten und es schien anfänglich nothwendig, entweder die beiden eben beschriebenen Schädel als *T. dyspelor* zu beschreiben, oder aus der hier als *T. proriger* angeführten Species, welche, wie oben gezeigt, sich bedeutend von *T. dyspelor* unterscheidet, eine neue Species zu machen. Es scheint mir jedoch, dass die Merkmale, die dem *T. proriger* zugeschrieben sind, nicht in allen Fällen ganz zutreffen. Wie Cope selbst erkannt hat, ist es möglich, dass die vermuthete vertical-elliptische Gestalt der Wirbel des *T. proriger* durch Druck veranlasst wurde; es ist wenigstens der auf Taf. 30 (Cretaceous Vertebrata) abgebildete Wirbel nicht sehr verschieden von einigen Wirbeln, die unzweifelhaft zu *T. dyspelor* gehören. Wie bekannt, kommt es häufig vor, dass Wirbel und andere Skelettheile durch Druck ausserordentlich verunstaltet werden, ohne diese Aenderung der Form durch Brüche zu zeigen. So existiren z. B. in der hiesigen Sammlung einige Rückenwirbel von *Platecarpus*, die seitlich bis zu einem Drittel des ursprünglichen Durchmessers zusammengepresst worden sind, aber kaum eine Spur von einer Spalte auf dem Gelenkkopfe zeigen. Auch scheint es etwas zweifelhaft, ob die Zahl der Zähne bei beiden Species verschieden ist, da das abgebildete Pterygoid von *T. proriger* nicht vollständig ist. Ich habe daher die Schädel, obwohl sie nicht genau mit der Beschreibung Cope's übereinstimmen, wegen ihrer Aehnlichkeit mit *T. proriger* zu dieser Species gestellt und glaube, dass sie dieser Art angehören.

T. micromus, Taf. I Fig. 3, ist die kleinste dieser drei Species und unterscheidet sich von den beiden anderen durch geringe Grösse, die leichter gebauten Knochen des Skelets und durch die Gestalt des Quadratum, welches einen etwas längeren Supracolumellar-Fortsatz und eine grössere Stapedialgrube hat und an der oberen inneren Ecke nicht so spitzig ist. Basioccipitale, Kiefer und Wirbel haben am meisten Aehnlichkeit mit *T. proriger* und das Pterygoid mit *T. dyspelor.*

Ausser den Arten, die in der Münchener Sammlung vertreten sind, werden noch folgende in den östlichen und westlichen Vereinigten Staaten angeführt:

Tylosaurus nepeolicus Cope. Hayden's Bull. U. S. Geol. Surv. of Territ 1874, p. 37.—Cretaceous Vertebrata 1875. Taf. 35 Fig. 11–13. Niobraragruppe, Kansas.

Tylosaurus (*Macrosaurus*) *laevis* Owen. Journ. Geol. Soc. London 1849, p. 380, Taf. 11.—*Liodon laevis* Cope. Extinct Batr. Rept. of N. A. 1870, p. 205. Greensand, N. Jersey.

Tylosaurus (*Geosaurus*) *Mitchellii* De Kay. Am. Lyc. of N. Y. III, p. 140.—*Mosasaurus Mitchellii* pro parte Leidy, Cret. Rept. of U. S. p. 65. Tafel 11.—*Drepanodon impar* Leidy Proceed. Acad. of Philad. 1856, p. 255.—*Lesticodus impar* Leidy. Geol. Surv. of N. Carolina p. 224, Fig. 45–46. Greensand, N. Jersey.

Tylosaurus validus Cope. Extinct Rept. of N. A. 1870, p. 207.—*Nectoportheus validus* Cope. Proceed. Acad. Nat. Sc. Philad. 1868, p. 181.—*Mosasaurus* pro parte Leidy, Cretac. Rept. of U. S. 1865, p. 74–75, Taf. 7, Fig. 19–20. 3, 1–2. Greensand, N. Jersey.

Tylosaurus sectorius Cope. Proceed. Amer. Phil. Soc. 1871, p. 41. Greensand, N. Jersey.

Tylosaurus perlatus Cope. Proceed. Amer. Phil. Soc. 1870, p. 497.—*Mosasaurus* "Gibbes" pro parte Cope. Extinct Batr. Rept. of N. A. 1870, p. 198. White Limestone, Alabama.

Liodon congrops Cope. Extinct Batr. Rept. of N. A. 1870, p. 206. Rotten Limestone, Alabama.

Genus Platecarpus Cope

Diese Gattung, womit das später von Marsh aufgestellte Genus *Lestosaurus* übereinstimmen dürfte, wurde von Cope für eine Pythonomorphen-Species mit einem breiten langen Quadratum und pleurodonten Pterygoidzähnen aufgestellt. Die Ueberreste dieses Genus scheinen zu den häufigsten Reptilresten in der Kansaskreide zu gehören; sie zeichnen sich gewöhnlich durch gute Erhaltung aus. Der *Platecarpus* stand in Bezug auf Grösse zwischen *Clidastes* und *Tylosaurus* und zeichnet sich durch einen etwas kürzeren, vorn nicht so spitzig ausgezogenen Schädel aus, der in der Regel eine Länge von ca. 50 cm hatte.

Die Münchener Sammlung enthält ausser dem wundervollen Schädel und der Wirbelsäule, die von BAUR[27] 1890 bei Russel Springs, Kansas gefunden und später beschrieben wurden, noch weitere sechs Skelete. Jedes derselben zeigt alle oder fast alle Theile des Kopfes, eine grosse Menge Wirbel und mehr oder weniger zahlreiche Extremitätenknochen. Eines dieser sechs Skelete hat eine vom Kopf bis fast zum Ende des Schwanzes vollständig geschlossene Wirbelsäule, desgleichen sind Schultergürtel, Beckengürtel und Extremitäten mit Ausnahme der Tarsalien, Carpalien und Phalangen vorhanden. Die Kopfknochen sind noch vollkommen im Zusammenhang. Im Uebrigen sind noch sehr viele Reihen von Wirbeln und vereinzelte Schädel- und Extremitätenknochen vorhanden.

Die Wirbelsäule zeigt in vielen Beziehungen grosse Aehnlichkeit mit der von *Tylosaurus*. So sind die Chevron-Bones gelenkig mit den Centren verbunden, das Zygosphen ist schwach entwickelt, und im Rücken- und Schwanzabschnitt scheint die Zahl der Wirbel mit der von *Tylosaurus* übereinzustimmen. Sie unterscheidet sich jedoch bedeutend von derjenigen des *Clidastes*, bei dem die Chevron-Bones mit den Centren verwachsen sind und das Zygosphen mächtig entwickelt ist.

Von den Halswirbeln, Taf. III Fig. 11, besteht der Atlas wie bei den anderen Gattungen aus dem Processus odontoideus, einem Basalstück mit zwei Seitenstücken, wozu auch eine grosse Hypapophyse kommt. Die Seitenstücke zeichnen sich meistens dadurch aus, dass sie am Hinterrande etwas ausgeschnitten sind und dass die hintere untere Ecke oft etwas ausgezogen ist, jedoch nicht so stark wie bei *Clidastes*. Die Hypapophyse des Atlas ist gross, reicht aber niemals so weit nach hinten, dass sie die Hypapophyse des

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[27] Journal of Morphology Vol. VII. Oct. 1892, p. 10.

Axis berührt. Der Epistropheus besitzt einen hohen, kräftigen, etwas nach hinten gerichteten Dornfortsatz, der oft hakenartig über das Rückenmark herüberragt. Hinten ist er mit zwei starken Zygapophysen versehen, zwischen welchen zwei seichte Vertiefungen zur Aufnahme des Zygosphens vorhanden sind. Die Ansatzstelle für das Endstück der Hypapophyse ist rundlich, nie oder selten vertieft und geht oft nahezu in den quer-elliptischen Gelenkkopf über. An den Seiten des Centrums sind zwei zapfenartige Fortsätze vorhanden, an welche sich das erste Paar der einköpfigen Rippen anlegte. Beim 5. Wirbel sind die Zygapophysen etwas grösser geworden, der Dornfortsatz steht fast vertical und die Diapophysen, die anfangs zapfenförmig waren, besitzen eine etwas S-förmig gebogene Ansatzfläche, deren unterer Theil nach vorn bis zum Rand der Aushöhlung des Centrums verläuft. Der Dornfortsatz des 7. (letzten) Halswirbels ist oben etwas breiter geworden und das Endstück der Hypapophyse entweder verschwunden oder mit der Basis verwachsen.

Die Rückenwirbel besitzen bis zum Schwanz Zygapophysen und ein schwaches Zygosphen; sie bleiben bis zur Mitte des Rückens fast gleich stark und werden nach hinten allmählich schwächer. Die am Anfang länglichen Diapophysen werden immer länger und im Querschnitt runder bis zu den Pygialwirbeln. Die Dornfortsätze werden langsam höher und breiter bis zum hinteren Drittheil des Rückens, alsdann aber wieder kleiner.

Auf die Dorsalwirbel folgen die Wirbel des Pygialabschnittes, die bei *Platecarpus* 7 an Zahl zu sein scheinen. Sie besitzen hohe breite Dornfortsätze, schwache Zygapophysen und lange, vertical zusammengedrückte Diapophysen. Mit Ausnahme des letzten, der ganz kleine Ansatzstellen für die Chevron-Bones besitzt, tragen sie keine Haemapophysen, zeigen jedoch fast immer auf der Unterseite mehrere characteristische Foramina, die in nicht so guter Entwicklung auch bei den letzten Rücken und ersten Chevron tragenden Wirbeln vorkommen.

Hinter den Pygialwirbeln trugen sämmtliche Schwanzwirbel geschlossene Haemapophysen, die mit den Centren gelenkig verbunden waren, und zeigten auch bis in den hinteren Theil des Schwanzes Diapophysen, die allmählich kleiner wurden, bis sie gänzlich verschwanden. Wie bei *Tylosaurus* und *Clidastes* hatten die Pygial und Chevron tragenden Schwanzwirbel den characteristischen eckigen Gelenkkopf, der sich im hinteren Theil des Caudalabschnittes zu der vertical-elliptischen Gestalt veränderte; jedoch war die eckige Form bei *Platecarpus* nicht so ausgesprochen, wie bei den anderen Gattungen.

Die Extremitäten, die denen von *Tylosaurus* sehr ähnlich sind, zeichnen sich durch den breiten Humerus und das kurze mit grossem Trochanter versehene Femur aus. Der Humerus ist kurz, abgeplattet und besonders am distalen Ende sehr breit. Unten, auf der Hinterseite des proximalen Endes ist er mit einer mässig hohen Crista versehen. Radius und Ulna sind beide breit und in der Mitte etwas verjüngt; der Radius ist fast immer am distalen Ende etwas breiter als am proximalen. Coracoid und Scapula haben grosse Aehnlichkeit mit denen von *Tylosaurus* und den Eidechsen, nur hat die Scapula, im Gegensatz zu der von *Tylosaurus* ungefähr die Grösse des Coracoideum. Das Coracoid hat meistens einen Einschnitt am Innenrand. Wenn jedoch *Holosaurus* Marsh, wie wahrscheinlich, mit *Platecarpus* identisch ist, kann es auch ganzrandig sein. Das Femur war nicht so breit wie der Humerus und mit einem grossen hohen Trochanter oder einer seitlichen Umbiegung des Vorrandes versehen. Tibia und Fibula wie das Femur waren oft viel dicker als die entsprechenden Knochen der Vorderextremitäten und zeigten in manchen Fällen sehr ungleiche Grösse; so konnte die Tibia zwei oder drei Mal so breit und viel dicker als die Fibula sein. Der Beckengürtel war fast genau wie der von *Tylosaurus* ausgebildet.

Der Schädel von *Platecarpus* zeichnet sich von dem anderer Gattungen durch seine verhältnissmässig grosse Höhe aus, was jedoch hauptsächlich der Verkürzung der Kiefer, die bei diesem Genus am kürzesten sind, zuzuschreiben ist.

Im Hinterhaupt, das im Allgemeinen mit dem anderer Genera übereinstimmt, unterscheidet sich das Basioccipitale, Taf. IV Fig. 2, von dem des *Tylosaurus* dadurch, dass seine Hypapophysen nicht seitlich zusammengedrückt sind und die hinteren Fortsätze des Basisphenoid sich nicht an ihrer Innenseite vorbeischieben, sondern nur an die Hinterseite anstossen. Auch besteht ein Unterschied in Bezug auf die Oberseite der Hypapophysen zwischen *Platecarpus* und *Tylosaurus* darin, dass die lappenartigen seitlichen Fortsätze des Ex-Occipitale sich bei *Platecarpus* bis zum Unterende des Hypapophyse hinüber erstrecken und ziemlich dick sind. Bei *Plate-*

carpus, wie bei *Plioplatecarpus* Dollo ist das Basioccipitale oft von einem mehr oder weniger grossen Loch durchbohrt.

Die Ex-Occipitalia, Taf. I Fig. 2 *Ex.*, zeichnen sich, wie oben erwähnt, durch ihre langen und dicken seitlichen Fortsätze aus.

Die hinteren Fortsätze des Basisphenoid, die gegen das Basioccipitale stiessen, waren nur wenig länger als die vorderen Pterygoidalprocessi. Infolge ihrer geringen Länge sind sie sich nicht an den Hypapophysen des Basioccipitale vorbeigeschoben.

Das Parietale, Taf. I Fig. 1 *Pa.*, hat eine sehr characteristische Gestalt. Es ist ziemlich kurz, in der Mitte verjüngt und hinten, wo die Arme auslaufen wieder etwas breiter. Auf der vorderen Hälfte der Oberseite zeigt es ein erhabenes Feld, an dessen Basis das nur sehr wenig oder gar nicht von der Coronalsutur entfernte Foramen parietale liegt. Die zwei herunterhängenden seitlichen Lappen oder Seitenränder des Parietale, die hinten sehr kurz sind und nicht mit einander verwachsen, waren gewöhnlich in ihrer ganzen Länge kurz und oft viel weiter ausgebreitet als bei *Tylosaurus.*

Das Frontale, Taf. I Fig. 1 *Fr.*, war hinten breit und herzförmig ausgeschnitten. Die Seitenränder waren über den Augenhöhlen meistens etwas eingebuchtet. Auf der Oberseite fehlte die characteristische Verzierung, die wir bei *Tylosaurus* kennen gelernt haben.

Das Postfrontoorbitale, Taf. I Fig. 2 *Ptf.*, das bei *Tylosaurus* so lang war, dass seine vordere Spitze über das Hinterende des Praefrontale hinüber reichte, ist bei *Platecarpus* vorn viel kürzer und greift nicht über das Hinterende des Praefrontale.

Der Kopf des Quadratojugale, Taf. IV Fig. 8, war hinten nicht oder doch nur sehr wenig heruntergebogen, der Oberflügel kurz und schmal und endigte oft spitz.

Das Quadratum, Taf. I Fig. 2 *Qu.*, Taf. III Fig. 3, 4, zeigte einen sehr langen Supracolumellar-Fortsatz, der nicht spitz auslief, sondern stumpf abgeschnitten war. Die vordere, innere Ecke ist oben fast immer abgerundet; zwischen ihr und dem Flügel ist der Oberrand der Vorderseite fast gar nicht eingebuchtet. Der obere Innenrand ist im Gegensatz zu *Clidastes* fast ganz gerade. Die grosse Stapedialgrube ist ebenso breit wie lang.

Die Praefrontalia, Taf. I Fig. 1 *Prf.*, Taf. III Fig. 5, weichen in ihrer Gestalt von den ziemlich regelmässig dreieckigen Praefrontalia des *Tylosaurus* beträchtlich ab, einmal dadurch, dass sich der Oberrand vor dem Vorderende seines Contactes mit dem Frontale steil herunterbiegt, anstatt gerade zu bleiben, und ferner dadurch, dass der Unterrand nicht gerade, sondern hinten tief eingebuchtet ist, wahrscheinlich um für die Lacrymalia Platz zu machen. Auf der Aussenseite des Vorderendes findet sich sehr häufig an der Stelle, an der die Spitze des Oberflügels des Maxillare sich anlegt, eine tiefe Rinne oder rinnenartige Grube zur Aufnahme derselben. Ein Theil des Hinterrandes ist wie bei *Tylosaurus* nach innen gebogen, um die hintere Wand der Nasenhöhle zu bilden; es ist jedoch nicht verdickt und nicht mit einer Längsrinne versehen, wie bei jenem, sondern bleibt dünn und scharf.

Ein Superciliare ist, wie im allgemeinen Theil erläutert wurde, wahrscheinlich nicht vorhanden.

Das Praemaxillare, Taf. I Fig. 1, 2 *Pmx.*, war nicht wie bei *Clidastes* und *Tylosaurus* schnabelartig verlängert, sondern vorn breit und an mehreren Exemplaren vor dem ersten Paar Zähne etwas eingekerbt. Der nach hinten gerichtete Stiel stand bis zum 3. Maxillarzahn mit dem Maxillare in Berührung und verjüngte sich von der Stelle, wo der Contact aufhörte, allmählich nach hinten bis zu der halben Länge der Nasenlöcher und wurde dann hinten, wo er mit den Nasalia verschmolz, wieder etwas breiter. Die Zähne, deren auf jeder Seite zwei vorhanden waren, sind im Querschnitt rundlich, aussen facettirt und schwach gestreift, innen stark gestreift.

Die Maxillen, Taf. I Fig. 2 *Mx.*, zeigen vorn sehr kurze, bis zum 3. Zahn reichende Ansatzflächen für das Praemaxillare; der Oberrand hinter dieser Fläche ist tief ausgeschnitten. Zwölf Zähne sassen auf meistens ziemlich weit hervorragenden Knochensockeln, waren im Querschnitt rundlich bis comprimirt und zeigten vorn und hinten eine Kante, die zuweilen auf der Hinterseite nur gegen die Spitze hin gut entwickelt ist. Auf der Innenseite waren sie stark gestreift und schwach facettirt, auf der Aussenseite stark facettirt und oft fast ohne alle Streifung.

Die Palatina, die wie bei *Tylosaurus* mit den Vomern verbunden waren, und in einer Rinne auf ihrer Aussenseite eine kleine Parthie des Innenrandes des Maxillare aufnahmen, waren viel leichter gebaut als bei jenem, besonders war der hintere Theil, welchem auf Praefrontale sass, viel dünner und oben immer zugeschärft.

Der Hauptheil (bezahnter Theil) des Pterygoids, Taf. I Fig. 2 *Ptg.*, ist etwas S-förmig gebogen und die ausgebreitete Parthie des Aussenrandes im Verhältniss zur Grösse des Knochens nicht so gross wie bei *Tylosaurus.* Der hintere Fortsatz, der das Pterygoideum mit dem Quadratum verband, ist am Anfang schmal und dick, in der Mitte dünn und ausgebreitet und wird am Hinterende wieder etwas schmäler, zeigt aber keinen Kopf am Hinterende wie bei *Tylosaurus.* Die 10 bis 12 Zähne haben eine etwas pleurodonte Befestigung, sind stärker gekrümmt und im Querschnitt etwas runder als die Kieferzähne, und besitzen hinten eine starke, vorne eine schwache Streifung und Andeutungen von Facettirung.

Das Transversum findet sich in einem Exemplar der Münchener Sammlung im Zusammenhang mit dem Pterygoid. Es zeigt im Allgemeinen dieselben Verhältnisse zu den anderen Knochen wie bei *Tylosaurus*; der Innenast ist jedoch meistens verdickt und nicht zweispitzig. Während die beiden Flächen auf der Oberseite des Innenastes bei *Tylosaurus* deutlich sind, können sie bei *Platecarpus* fast nicht unterschieden werden.

Lacrymale. An einem der mir vorliegenden Exemplare liegt auf dem Hinterende des Maxillare und zwischen diesem und dem Praefrontale eine unregelmässig gestaltete Masse, die wie bei *Tylosaurus* sich durch ihre punktirte Oberfläche auszeichnet und unzweifelhaft das Lacrymale darstellt. Bei einem anderen Exemplar lag auf dem macerirten Praefrontale eine vierseitige Platte, die auf dem einen Rand einen kleinen tiefen Ausschnitt zeigt. Da sie ziemlich hoch auf der Seite des Praefrontale lag, war der erste Gedanke, es sei das Superciliare, da aber der eine Rand einen Einschnitt aufweist, und die Seiten höckerig sind, ist es wahrscheinlicher, dass die Platte ein durch Maceration frei gewordenes Lacrymale ist.

Mandibeln, Taf. I Fig. 2. Das Vorderende des Dentale von *Platecarpus* war schmal, der erste Zahn stand dicht an demselben. Das Zahnbein war, wie das Maxillare mit 12 Zähnen besetzt, die denen der letzteren ähnlich sind. Im Verhältniss zur Länge des Supraangulare war das Coronoideum nicht ganz so lang wie bei *Tylosaurus* und viel kürzer als bei *Clidastes*, auch war sein hinterer

Flügel weder so hoch noch auf der Aussenseite so tief ausgehöhlt wie bei diesen beiden Gattungen.

Die übrigen Schädelknochen von *Platecarpus* weichen nur unerheblich von denen des *Tylosaurus* ab, es erscheint ihre nähere Beschreibung daher nicht als nothwendig.

Die Gattung *Platecarpus* enthält 13 Arten, deren Characterisirung zum grossen Theil nicht genügend und nur auf dürftigen Resten basirt ist. Diese Species scheinen, wenn es deren überhaupt so viele giebt, wie angegeben wird, sehr variabel zu sein. In der Münchener Sammlung sind die verschiedenen Formen von Quadratbeinen, Basioccipitalia, Pterygoidea, Parietalia, Zähnen etc., welche die Speciesmerkmale liefern, so mannichfaltig, aber auch so sehr durch Uebergangsformen verbunden, dass man entweder noch eine ganze Menge neuer Species aufstellen oder besser ihre Zahl auf wenige Typen reduciren müsste. Diese Frage könnte aber nur durch eine eingehende Untersuchung des Materials in den verschiedenen americanischen Sammlungen zur Entscheidung gebracht werden. Unter dem Material des Münchener Museums sind folgende Arten zu erkennen: *P. coryphaeus* COPE, *P. ictericus* COPE, *P. simus* MARSH, *Platecarpus oxyrhinus* nov. spec.

P. coryphaeus, Taf. I Fig. 1, 2, ist durch die Wirbelsäule und durch *P. clidastoides* nov. spec., den ausserordentlich schönen Schädel, welcher schon von Prof. BAUR genau beschrieben wurde, sowie durch viele andere, sehr gut erhaltene Exemplare vertreten. Die wichtigsten Merkmale, wodurch diese Art sich von den anderen unterscheidet, sind die kurze, vorne oft eingekerbte Schnauze, das breite Parietale mit grossem, weit vorne liegendem Scheitelloch, die tiefe Grube auf der Aussenseite des Praefrontale, die zur Aufnahme der Spitze des Oberflügels des Maxillare dient, der breite, flache, leicht gebaute, mit kleiner Crista versehene Humerus und die etwas grösseren Zähne. Ausser den eben angeführten Ueberresten, die zu *P. coryphaeus* gestellt wurden, befinden sich in der Sammlung von einem anderem sehr grossen Individuum eine Reihe von Schwanzwirbeln und einige Dorsalwirbel, die sämmtlich sehr zerquetscht sind, ferner ein vollständiger Beckengürtel mit Femur, ein Humerus mit Radius, Ulna, Carpalien, Metacarpalien und Phalangen und vom Schädel das Quadratum, Basisphenoid und

Basioccipitale, worunter sich die Extremitätentheile durch sehr gute Erhaltung und Vollständigkeit auszeichnen. Der Humerus ist sehr gross. Ilium, Ischium, Pubis und Femur haben grosse Aehnlichkeit mit den entsprechenden Knochen von *P. simus*, es ist jedoch der Processus am proximalen Ende des Pubis grösser, als bei diesem und am Ischium ist der obere Theil der Ausbreitung nach hinten spitzer ausgezogen. Der Trochanter des Femur ist im Gegensatz zu *P. simus* sehr hoch und reicht von der einen Seite bis fast zur anderen herüber. Das Quadratum stimmt mit dem von *P. coryphaeus* überein. Es scheint zweckmässiger, diese Reste zu dieser Species zu stellen, als eine schlecht characterisirte Art daraus zu machen.

P. simus Marsh ist durch die Extremitäten und eine vom Rücken bis zum Hinterende des Schwanzes vollständige Reihe von Wirbeln vertreten. Er unterscheidet sich von *P. coryphaeus* dadurch, dass der Trochanter des Femur neben dem Rande steht[28] und nicht sehr lang ist.

P. ictericus Cope ist durch einen Schädel mit dem grössten Theil der Wirbelsäule vertreten. Er unterscheidet sich von den anderen Arten durch das sehr schmale Parietale, durch das Praefrontale, das anstatt einer Grube zur Aufnahme der Spitze des Oberflügels des Maxillare nur eine seichte Rinne besitzt, durch das Quadratum, welches einen verhältnissmässig kurzen Supracolumellar-Fortsatz eine sehr niedere oder keine Submeotalleiste und eine tiefe kurze Stapedialgrube hat, und durch die Zähne, welche meistens kleiner und schlanker sind.

P. clidastoides nov. spec. Die Aufstellung dieser Species stützt sich auf ein Parietale, das ganze Hinterhaupt, das Quadratojugale, den Atlas, einige Dorsal- und 3 Caudalwirbel. Sie characterisirt sich durch das eigenthümliche Parietale, das vorn ein niedriges dreieckiges Feld zeigt, in dessen Mitte das verhältnissmässig kleine, runde, von der Coronalsutur weit entfernte Scheitelloch liegt. Am Hinterende ist das Scheitelbein vertical verflacht und zeigt grosse Aehnlichkeit mit dem von *Clidastes*. Das ganze Aussehen dieses Knochens ist durchaus verschieden von dem der anderen *Platecarpus*-Species. Die Zugehörigkeit zu dieser Gattung wird jedoch durch das durchbohrte Basioccipitale und das *Platecarpus*-ähnliche

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[28] Structure of Mosasauroid Reptiles Marsh. Amer. Journ. Science 1872, p. 464, Taf. 12 Fig. 2 a.

Seitenstück des Atlas bewiesen. Die Wirbel sind so zerquetscht und verwittert, dass sie weder als *Platecarpus*- noch *Clidastes*-ähnlich zu erkennen sind.

P. oxyrhinus nov. spec. Die Art beruht auf zwei Oberkiefern, einer Praemaxilla, Stücken vom Dentale, Transversum, Femur und Ulna. Das Merkmal, wodurch sie sich bedeutend von allen anderen Arten unterscheidet, ist die Verlängerung der Schnauze, wie bei *Clidastes*, nur ist diese Verlängerung nicht so bedeutend, wie bei letzterer Gattung.

Von *Platecarpus*-Arten, die in America vorkommen, werden folgende citirt:

Platecarpus tympanicus Cope. Cretac. Vertebr. 1875, Taf. 37, Fig. 11.—Proceed. of Boston Soc. of Nat. Hist. 1869, p. 265. —Extinct Batr. and Rept. of N. A. 1870, p. 200.—*Holcodus acutidens* "Gibbes" Leidy, in part, Cret. Rept. of U. S., p. 118, Taf. 7, 8, 11. Cretaceous, Mississippi.

Platecarpus (*Lestosaurus*) *felix* Marsh. Amer. Journ. of Sc. and Arts 1872, June, Taf. 8, Fig. 4. Niobrara, Kansas.

Platecarpus (*Lestosaurus*) *simus* Marsh. Amer. Journ. of Sc. and Arts 1872, p. 455, Taf. 10, 12. Niobrara, Kansas.

Platecarpus (*Lestosaurus*) *latifrons* Marsh. Amer. Journ. of Sc. and Arts 1872, p. 458. Niobrara, Kansas.

Platecarpus (*Lestosaurus*) *gracilis* Marsh. Amer. Journ. of Sc. and Arts 1872, p. 460. Niobrara, Kansas.

Platecarpus curtirostris Cope. Cretac. Vertebr. 1875, p. 150, Taf. 14, 15, 16, 17, 18, 21, 36, 37, 38. Niobrara, Kansas.

Platecarpus (*Liodon*) *latispinis* Cope. Cret. Vertebr. 1875, p. 155, Taf. 26.—Proceed. Amer. Philos. Soc. 1871, p. 169.

Platecarpus (*Liodon*) *glandiferus* Cope. Cretac. Vertebr. 1875, p. 156, Taf. 26.—Proceed. Amer. Phil. Soc. 1871. Niobrara, Kansas.

Platecarpus (*Liodon*) *crassartus* Cope. Cretac. Vertebr., p. 153, Taf. 16.—Proceed. Amer. Philos. Soc. 1871, p. 168. Niobrara, Colorado.

Platecarpus (*Liodon*) *Mudgei* Cope. Cretac. Vertebr., p. 157, Taf. 16, 17, 26, 37.—Proceed. Amer. Philos. Soc. 1870, p. 581.—*Holcodus Mudgei* Cope. Proceed. Amer. Philos. Soc. 1871. Niobrara, Kansas.

Platecarpus (*Holcodus*) *tectulus* Cope. Cretac. Vertebr., p. 159, Taf. 21, 27.—Proceed. Amer. Philos. Soc. 1871. Niobrara, Kansas.

Genus Clidastes Cope

Dieser Gattung gehören die schlankesten und in ihrer äusseren Erscheinung schlangenartigsten Pythonomorphen an. Sie unterscheidet sich von den anderen Gattungen durch die Zahl der Zähne (Maxillare 17, Dentale 18 und Pterygoid 15) durch die ausgezeichnete Entwickelung des Zygosphens und die mit den Wirbelcentren verwachsenen Chevron-Bones. Das für einige Pythonomorphen-Reste von Marsh aufgestellte Genus *Edestosaurus*, das sich von *Clidastes* durch den Grad der pleurodonten Befestigung der Zähne unterscheiden soll, scheint mit *Clidastes* identisch zu sein.

Obwohl die Münchener Sammlung an gut erhaltenen Ueberresten der Gattung *Clidastes* nicht ebenso reich ist, wie bei den anderen Gattungen, enthält sie doch immerhin eine Anzahl sehr werthvoller Skelete und Theile derselben. So liegen von einem Exemplar der ganze Schädel und die Wirbelsäule bis zum Schwanz vollständig vor, ein zweites zeigt fast den ganzen Schädel, die nahezu vollzählige Wirbelsäule und die meisten Knochen der Vorderextremitäten. Ausserdem sind noch Theile von Schädeln, Wirbelsäulen und Extremitäten von 12 Individuen vorhanden, die einander ergänzen und die ganze Osteologie klarstellen.

Die Wirbelsäule unterscheidet sich, wie eben bemerkt, von der aller anderen Pythonomorphen durch das kräftige Zygosphen und die Befestigung der Haemapophysen, im Besonderen differirt sie von *Tylosaurus* und *Platecarpus* durch die Zahl der Rücken- (35) und Schwanzwirbel (74).

Unter den Halswirbeln, Taf. III Fig. 9, zeichnet sich der Atlas durch seine Seitenstücke aus, welche am Hinterrande dick und an der unteren, hinteren Ecke in einen ziemlich langen Fortsatz ausgezogen sind. Der Epistropheus zeigt einen kräftigen, nach hinten gerichteten Fortsatz und zwei grosse Postzygapophysen, die zwischen sich tiefe Aushöhlungen zur Aufnahme der beiden Hälften des Zygosphens aufweisen. Die Hypapophysen der Halswirbel, deren Endglieder zuweilen mit den Basen verwuchsen, waren meistens im Vergleich zu denen der anderen Genera lang. Am 4. Wirbel sind die Diapophysen, die am Epistropheus sehr kurz und klein sind, länger und breiter geworden, und die Ansatzstellen für die Rippen S-förmig gebogen, wobei sich der Untertheil der Diapophyse nach vorn biegt und mit dem Vorderrand des Centrums zusammenfliesst. Die Hypapophyse des 7. Wirbels ist klein geworden, sie zeigt nur eine ganz kleine Ansatzstelle für das Endstück, welches möglicherweise gefehlt hat. Das Zygosphen und die Zygapophysen sind kräftiger geworden und der jetzt fast vertical stehende Dornfortsatz etwas breiter. Der 8., der erste Dorsalwirbel trägt unten einen grossen Höcker, der ebenso gross ist, wie der Rest der Hypapophyse des 7. Wirbels von *Platecarpus*. Ebenso zeigt der 9. Wirbel einen deutlichen Höcker, den Rest einer Hypapophyse.

Sämmtliche Rückenwirbel haben kräftige Zygapophysen und Zygosphen, während die an den letzten Halswirbeln flügelartig ausgebreiteten Diapophysen allmählich schmäler, länger und im Querschnitt runder werden.

Die ersten Schwanzwirbel (Pygialwirbel) unterscheiden sich von den letzten des Dorsalabschnittes, wie bei den anderen Gattungen dadurch, dass die Diapophysen länger und schmäler werden, die noch rundlichen Gelenkköpfe der Rückenwirbel eine eckige Gestalt annehmen, und wie bei *Tylosaurus* auf der Unterseite zwischen den Diapophysen sich drei deutliche Facetten zeigen. Hinter dem Pygialabschnitt sind sämmtliche Caudalwirbel mit Chevron-Bones (Haemapophysen) versehen, welche ohne Ausnahme mit den Wirbelcentren verwachsen sind. Am vorderen und mittleren Theil des Schwanzes zeigen die Wirbel meist ziemlich hohe, dünne, vorn und hinten zugeschärfte Dornfortsätze, die zusammen mit den Centren und den langen Haemapophysen den Schwanz zu einem mächtigen, vertical gestellten Ruderorgan umgewandelt haben. Die Chevron tragenden Caudalwirbel wiesen wie die Pygialwirbel Diapophysen auf, die jedoch nach hinten kleiner wurden und auf der Seite des Centrums etwas heraufrückten, bis sie endlich zu kleinen, an der Mitte des Centrums stehenden Höckerchen wurden und weiter hinten ganz verschwanden.

Die Extremitäten, die Williston und Case[29] ausführlicher beschrieben, haben in der Form der Schulter- und Beckengürtel grosse Aehnlichkeit mit denen von *Platecarpus*. Sie weichen aber im Beckengürtel dadurch ab, dass der bei *Platecarpus* breite Untertheil des Ischium etwas schmäler ist. Der Humerus ist für das Genus *Clidastes* characteristisch. Er ist sehr kurz, fast so breit wie lang, abgeplattet und trägt eine kleine von der unteren Ecke des proximalen Endes nach innen verlaufenden Crista. Das distale Ende, dessen Breite fast der Länge des ganzen Humerus gleichkommt, besitzt auf der Unterseite einen rundlichen, am Ende gerade abgestutzten Fortsatz und ragt auf der Oberseite ungefähr wie bei *Platecarpus* hervor, ist aber mehr angeschwollen. Radius und Ulna sind kurze, gedrungene Knochen, die an den Enden etwas erweitert sind. Die Ulna ist am proximalen Ende etwas breiter als am distalen und der Radius distal fast zwei Mal so breit wie proximal. Die Handwurzel bestand aus zwei Reihen von Knöchelchen, von denen die proximale 4, die distale 3 enthielt. Die Phalangen scheinen nach Marsh annähernd die Formel 3, 5, 5, 4, 3 gehabt zu haben und waren wie bei den Walen weit ausgebreitet. Das Femur, welches sehr wenig von dem der anderen Pythonomorphen abweicht, war schlanker und schmäler als der Humerus, am distalen Ende am breitesten und hatte einen proximalen Trochanter. Die Tibia war grösser als die Fibula und am Unterrande etwas ausgebuchtet. Die Fibula war am proximalen Ende sehr klein, am distalen Ende jedoch ungefähr $\frac{3}{4}$ so breit wie die Tibia. Die Tarsalien und Phalangen sind bis jetzt nicht vollständig bekannt; Williston und Case haben jedoch Femur, Tibia, Fibula mit Tarsalien abbilden können.

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[29] Quart. Kansas Univ. Vol. I. July 1892, p. 15.

Der Schädel von *Clidastes* hatte unter allen Pythonomorphen-Gattungen die grösste Länge und zeichnet sich besonders durch seine sehr langen Kiefer und Flügelbeine aus, die auch die grösste bekannte Zahl von Zähnen besitzen. Die Hypapophysen des Basioccipitale, die im Querschnitt nicht ganz regelmässig sind, zeigen vorn eine oft etwas grössere Breite als hinten. Die seitlichen Fortsätze der Ex-Occipitalia die sich an die Hypapophysen anlegten, reichten fast bis zum unteren Ende, waren aber dünn und am distalen Ende nicht so breit wie bei *Platecarpus*; sie stehen infolgedessen bezüglich ihrer Grösse zwischen *Tylosaurus* und *Platecarpus*. Beim Basisphenoid waren die hinteren Fortsätze sehr kurz und stiessen an die Hinterseite der Hypapophysen. Das Parietale war vorn sehr breit, ebenso breit wie das Hinterende des Frontale und verjüngte sich nach hinten allmählich. Von der

Unterseite gingen zwei grosse breite Lappen aus, die wie bei *Tylosaurus* von den vorderen Ecken nach hinten verliefen. Die Lappen breiteten sich vorn oft fast horizontal aus und erscheinen als zwei breite Flügel an beiden Seiten des Scheitelbeines; hinten, wo sie auf dem Occipitale superius auflagen, scheinen sie fast verschwunden zu sein. Die obere Fläche des Parietale war wie bei *Tylosaurus* ganz flach und die Basen der Arme lagen hinten in demselben Niveau wie der Vordertheil der Oberseite. Das kleine Scheitelloch war ziemlich weit von der Coronalsutur entfernt. Das Frontale war meistens sehr lang, in der vorderen Hälfte schmal, hinten fast gerade abgestutzt, mit der Ausnahme, dass es auf jeder Seite einen etwas entfernt vom Mittelpunkt des Hinterrandes liegenden zackigen Vorsprung trug. Ueber den Augenhöhlen waren die Seitenränder ausgeschnitten; Nebenspitzen waren meistens nicht vorhanden.

Die Postfrontoorbitalia waren gegen die von *Platecarpus* und *Tylosaurus* vorn sehr kurz und häufig durch eine grosse Lücke von dem Hinterende der Praefrontalia getrennt. Infolgedessen nahm das Frontale an der Begrenzung der Augenhöhlen theil. Hinter dem Frontale war gewöhnlich die Naht zwischen dem Postfrontoorbitale und dem Seitenflügel des Parietale sichtbar.

Das Quadratum, Taf. III Fig. 6, 7, das im Verhältniss zur Grösse des Schädels viel kleiner ist, als bei *Platecarpus*, zeichnet sich durch seine gedrungene Form und die Festigkeit seines Baues aus. Der kurze äussere Flügel bleibt bis zu dem nicht stark angeschwollenen Aussenrande dick und ist infolgedessen fast immer ganz erhalten, während bei *Tylosaurus* und *Platecarpus* die dünne, mittlere Parthie des Flügels fast immer weggebrochen ist, selbst wenn der wulstige Rand erhalten bleibt. Der kurze Supracolumellar-Fortsatz hat ungefähr die Länge des von *Tylosaurus*, ist jedoch im Gegensatz zu diesem am Ende breit. Der obere Vorderrand des Quadratum ist nach vorn etwas concav, und der Innenrand des Oberendes an der Basis des Supracolumellar-Fortsatzes tief eingebuchtet. Die Stapedialgrube ist elliptisch oder oval.

Die Gestalt der Praefrontalia, Taf. III Fig. 10, variirt bei den verschiedenen Species erheblich. Mit den von *Tylosaurus* haben sie den fast geraden Ober- und Unterrand gemeinsam, unterscheiden sich jedoch dadurch, dass meistens ein grosser, horizontal gestellter Lappen hinten vom oberen Rand ausgeht und horizontal neben dem Frontale steht. Bei einigen Species, *C. velox*, *C. tortor*, ist diese Ausbreitung so gross geworden, dass fast das ganze Praefrontale aus ihr besteht, während die ursprüngliche Aussenwand des Praefrontale senkrecht von der Unterseite desselben herunterhängt. Das Praemaxillare, Taf. I Fig. 4 *Pmx.*, nimmt in Bezug auf seine Gestalt eine Mittelstellung zwischen *Tylosaurus* und *Platecarpus* ein. Es war vorn etwas schnabelartig ausgezogen, aber nicht so sehr wie bei *Tylosaurus* und endete spitz, anstatt gerade abgeschnitten wie bei diesem. Der lange, nach hinten gerichtete Stiel stand bis zum 6. Maxillar-Zahn in Berührung mit dem Maxillare und war bis zu dieser Stelle fast gleichmässig breit; er verjüngte sich dann langsam nach hinten bis zur Mitte des Nasenloches. Wie bei *Tylosaurus* gingen von dem bezahnten Theil zwei Fortsätze nach hinten aus, die die Vorderenden der Vomera aufnahmen.

Die Maxillaria, Taf. I Fig. 4 *Mx.*, sind sehr lang und schlank und vorn bis zum 6. Zahn von der Ansatzfläche des Praemaxillare schräg abgestutzt. Auf dem Oberrand ist nur eine schwache Concavität an der Stelle vorhanden, an der bei *Platecarpus* der Rand ziemlich tief ausgeschnitten ist. Auf ihnen sassen 17 Zähne, die rundlich bis comprimirt waren. Andeutungen einer Facettirung sind zuweilen zu sehen, eine Streifung scheint selten vorhanden zu sein.

Das Palatinum ist infolge der Verlängerung des Oberkiefers sehr lang. Auf der Aussenseite verläuft eine tiefe Rinne zur Aufnahme des Kieferrandes; am Hinterende vermittelte ein dicker, oben meistens abgestutzter Fortsatz die Verbindung mit dem Praefrontale.

Wie die Kiefer; so sind auch die Pterygoidea, Taf. I Fig. 4 *Ptg.*, ausserordentlich lang und schlank. Der bezahnte Theil war fast gerade, auf der Oberseite etwas ausgehöhlt, und zeigte 15 etwas pleurodonte, wenig comprimirte, fast glatte Zähne. Die beiden Fortsätze, die das Pterygoid mit dem Transversum und dem Quadratum verbinden, entspringen am hinteren Drittheil des bezahnten Theiles. Der Fortsatz, der nach dem Quadratum ausgeht, ist wie bei *Platecarpus* am Anfang und am Hinterende verjüngt, in der Mitte aber etwas ausgebreitet.

Mandibeln, Taf. I Fig. 4. Die Zahnbeine waren vorn schmal und meistens abgerundet. Sie trugen die grösste bis jetzt bei

Pythonomorphen bekannte Zahl von Zähnen, nämlich 18. Die Zähne waren, wie die auf dem Maxillare rundlich bis comprimirt und hatten vorn eine scharfe Kante. Eine zweite Kante stand bei den hinteren Zähnen auf der Mitte der Hinterseite und rückte auf den vorderen Zähnen nach der Aussenseite hin. Sehr schwache Facettirung kommt zuweilen vor, Streifung ist sehr selten zu beobachten. Die hinter der Gelenkpfanne gelegene Parthie des Articulare war nicht so breit wie bei *Tylosaurus* und *Platecarpus*, sondern ihr Unterrand war fast horizontal, ihr Oberrand schräg nach unten und der Hinterrand vertical abgeschnitten. Der Theil des Oberrandes des Supraangulare zwischen der Gelenkpfanne und dem Hinterende des Coronoideum betrug nicht ganz die Hälfte der Länge des ganzen Oberrandes und war dünner als bei den anderen Gattungen.

Dieser Gattung scheint eine Reihe guter Arten anzugehören, die sich zum Theil durch das variabel Praefrontale, zum Theil durch das Quadratum, Frontale, Pterygoid und die Wirbel von einander unterscheiden. Unter dem Material, welches mir von *Clidastes* vorliegt, sind vier Arten vorhanden: *C. velox* MARSH, *C. medius* nov. spec., *C. liodontus* nov. spec. und sechs Individuen von *C. pumilus* MARSH.

C. velox MARSH, Taf. I Fig. 4, hat mit *C. tortor* besonders die eigenthümliche Entwickelung des Praefrontale gemeinsam. Wie in der Beschreibung erwähnt wurde, ist die Aussenseite dieses Knochens hinten unter dem Oberrand stark verbreitert. Diese Verbreiterung steht horizontal neben dem Frontale und bewirkt, dass der vordere Theil des Kopfes viel breiter als bei einigen anderen Species dieses Genus ist. Es ist auch bei dieser Art das Coracoid am Innenrand ausgeschnitten, was bei *C. tortor* nicht vorkommen soll.

C. medius nov. spec. Diese Species beruht auf dem grössten Theil eines Schädels, den Halswirbeln und den vier ersten Rückenwirbeln. Die meisten Knochen stimmen mit den entsprechenden von *C. velox* und *tortor* überein, unterscheiden sich aber dadurch, dass das Praefrontale nicht so weit in der Entwickelung zu einer einfachen horizontalen Platte vorgeschritten ist, sondern ist wie bei *Platecarpus* das Hinterende mit einer nach hinten gerichteten, unten abgerundeten oberen Ecke versehen, aus deren Aussenseite der fast horizontal gestellte Lappen entspringt. Der Lappen hat an diesem

Exemplar das ursprüngliche Hinterende von oben herunter umwachsen, doch ist die Grenze zwischen dem Lappen und dem Kopf sehr deutlich. Auch ist die vertical stehende Aussenseite des Knochens, die mit der Maxillare in Verbindung steht, grösser als bei *C. tortor*. Es scheint diese Species ein Verbindungsglied zu sein zwischen *C. stenops*, bei welchem das Praefrontale mehr *Tylosaurus*-ähnlich ist, und *C. tortor*.

C. liodontus nov. spec. Diese Art ist in der Münchener Sammlung durch die fast vollständigen, jedoch sehr zerstückelten Oberkiefer, Zwischenkiefer und das Dentale vertreten. Das Praemaxillare ist in eine spitze Schnauze ausgezogen und besitzt vier, an der Basis rundliche Zähne, die vorn eine ziemlich starke und auf dem hinteren Drittheil der Aussenseite eine sehr schwache Kante zeigen. Die Maxillen sind vorn bis ungefähr zum 5. Zahn von dem Praemaxillare schräg abgeschnitten. Vorn sind die Maxillarzähne wie die des Dentale an der Basis rundlich und gegen die Spitze comprimirt, mit einer starken Kante vorn und einer etwas seitlich gelegenen hinten. Nach dem Hinterende der Kiefer werden die Zähne stärker zusammengedrückt und sind an dem hinteren Theil desselben stark comprimirt. Am Ober-, Unter- und Zwischenkiefer sind alle Zähne ganz glatt und könnten mit denen von *Liodon* Owen verglichen werden, von welchen sie sich kaum, oder gar nicht unterscheiden.

C. pumilus Marsh zeichnet sich besonders durch seine geringe Grösse aus, welcher Eigenschaft wohl ein specifischer Werth beizulegen ist, weil man sonst annehmen müsste, dass Individuen mit der geringen Schädellänge von 22 cm zu derselben Species gehören, wie die grossen Exemplare von *C. velox*.

Ausser den erwähnten Species kommen folgende in den Vereinigten Staaten vor:

Clidastes planifrons Cope. Hayden's Bull. of U. S. Geol. Surv. Nr. 2, 1874, p. 31.—Cretaceous Vertebrata Vol. II 1875, p. 135, Taf. 22 und 23.

Clidastes tortor Cope. Cretaceous Vertebrata Vol. II 1875, p. 131, Taf. 14, 16, 17, 19, 36 u. 37.—*Edestosaurus tortor* Cope. Proceed. Amer. Philos. Soc. Dec. 1871. Niobrara, Kansas.

Clidastes stenops Cope. Cretac. Vertebr. Vol. II 1875, p. 133, Taf. 14, 17, 18, 36, 37, 38.—*Edestosaurus stenops* lc. HAYDEN'S nn. Report U. S. Geol. Surv. 1871, p. 330. Niobrara, Kansas.

Clidastes rex MARSH. Amer. Journ. Sc. and Arts 1872, June. Niobrara, Kansas.

Clidastes affinis LEIDY. Report U. S. Geol. Surv. of Territ. I, p. 281, Taf. 34. Niobrara, Kansas.

Clidastes (*Edestosaurus*) *dispar* MARSH. Amer. Journ. Sc. and Arts 1871, June. Niobrara, Kansas.

Clidastes velox MARSH. Amer. Journ. Sc. and Arts 1871, p. 450. Niobrara, Kansas.

Clidastes Wymani MARSH. Amer. Journ. Sc. and Arts 1871, p. 451. Niobrara, Kansas.

Clidastes pumilus MARSH. Amer. Journ. Sc. and Arts 1871, p. 452.

Clidastes cineriarum COPE. Cretac. Vertebr. II, p. 137, 1875, Taf. 21.—Proceed. Amer. Phil. Soc. 1870, p. 583. Niobrara, Kansas.

Clidastes propython COPE. Proceed. of Boston Soc. of Nat. hist. 1869, p. 258.—Extinct Batr. and Rept. of N. A. 1870, p. 221, Taf. 12. Rotten limestone, Alabama.

Clidastes iguanavus COPE. Proceed. Acad. of Philadelphia 1868, p. 223.—Extinct Batr. and Rept. of N. A. 1870, p. 220, Taf. V. Greensand, N. Jersey.

Clidastes intermedius LEIDY. Proceed. Acad. of Philad. 1870. —Report U. S. Geol. Surv. of Territ. 1873, I, p. 281, Taf. 34. Rotten limestone, Alabama.

BAPTOSAURUS MARSH

Unter dem von Herrn STERNBERG gesammelten Material fanden sich in einer Kiste einige Wirbel und Schädelknochen von gleichartiger Erhaltung. Sie gehörten wahrscheinlich zu demselben Individuum. Das einzige Kieferstück, Taf. IV Fig. 10, das vorne ungefähr in der Mittellänge des Coronoideums abgebrochen ist, stimmt bis auf das abweichende Articulare mit dem von *Platecarpus* oder *Tylosaurus* überein, unterscheidet sich jedoch von diesen dadurch, dass der Oberrand des Articulare unmittelbar hinter der Gelenkpfanne, anstatt sich um etwa 40° nach unter zu biegen, vertical herauf in einen hohen Fortsatz ausgezogen ist. Dadurch erhält das Hinterende des Unterkiefers ein hakenartiges Aussehen.

Auch an der unteren hinteren Ecke, wo bei *Platecarpus* und *Tylosaurus* eine längliche Verdickung verhanden ist, verdickt sich der Rand plötzlich um mehr als zwei Mal der Dicke hinter dieser Stelle und wird dann plötzlich unter dem Hinterende der Gelenkpfanne dünner. Es liegen 3 Hals- und 5 Rückenwirbel vor. Die Halswirbel, Taf. IV Fig. 9, besitzen kräftige, breite Zygapophysen, wovon die vorderen ziemlich nach oben gerichtet sind, und kein Zygosphen zwischen sich hatten. Nur zwischen den vorderen Zygapophysen ist die Oberseite des Neuralcanals dachförmig nach vorn ausgedehnt, und verbindet die Zygapophysen durch eine gebogene Lamelle; ein eigentliches Zygosphen wird jedoch nicht gebildet. Die Diapophysen sind sehr lang und vorn ausgehöhlt. Sie gehen, von hinten gesehen, fächerartig vom Centrum aus, wobei der Oberrand horizontal und in demselben Niveau mit der Oberseite des Centrums steht, während der Unterrand schief nach unten verläuft und so veranlasst, dass die untere Ecke der Diapophyse sehr viel tiefer steht, als die Unterseite des Centrums, eine Erscheinung, die bei keiner anderen Gattung so auffallend wie bei dieser ist. Die Unterseite des Centrum ist mit einem hohen Kiel, an dessen Hinterende die Hypapophyse steht, versehen. Der Gelenkkopf, resp. das Centrum, ist in der verticalen Richtung stark zusammengedrückt. Der verticale Durchmesser des Gelenkkopfes des mittleren der drei Halswirbel beträgt 24 mm, der transversale 42 mm.

Von den Rückenwirbeln gehört der eine offenbar in die Nähe des Halses, da das Centrum unten einen hohen abgerundeten Kiel besitzt. Die Diapophysen sind breit und gehen von der Seite des Centrums aus. Die dachförmige Verlängerung der Oberseite des Neuralcanals ist etwas stärker als bei den Halswirbeln. Die Gelenkköpfe der anderen Dorsalwirbel, die wahrscheinlich aus verschiedenen Theilen des Rückens herrühren, sind rundlicher und die Diapophysen etwas höher heraufgerückt. Hieraus könnte man schliessen, dass die Wirbel nach hinten ihre zusammengedrückte Gestalt verlieren, wobei die Diapophysen zugleich weiter heraufrücken.

Ein Stück des Hinterendes des Praefrontale hat viel Aehnlichkeit mit dem von *Tylosaurus*, nur ist auf der Aussenseite desselben keine tiefe Rinne zur Aufnahme des spitzen Vorderendes des Postfrontoorbitale vorhanden. Es liegt auch ein sehr zerquetschtes

Quadratum vor, das einen Supracolumellar-Fortsatz, der dem von *Platecarpus* sehr ähnlich sieht, besitzt. Der Flügel des Quadratums ist wie bei *Platecarpus* und *Tylosaurus* in der Mitte sehr dünn und durchbrochen.

Diese Wirbel und Knochen unterscheiden sich so erheblich von denen der anderen Genera, dass zuerst der Aufstellung eines neuen Gattungsnamens nothwendig schien. Da jedoch die Wirbel grosse Aehnlichkeit mit denen von *Baptosaurus* MARSH zeigen, ist es möglich, dass sie dieser Gattung angehören. Um eine unnöthige Vervielfältigung der Zahl der Gattungen zu vermeiden, entschloss ich mich, sie zu diesem Genus zu stellen und mit Rücksicht auf das hackenartige vorspringende Articulare ihnen den neuen Speciesnamen *onchognathus* beizulegen.[30]

Von der Kreide von N. Jersey werden folgende zwei Species angeführt:

Baptosaurus (*Macrosaurus*) *platyspondylus* MARSH. Amer. Assoc. of Sc. Salem Meeting, August 1869.—Amer. Journ. Science 1869, p. 195.

Baptosaurus fraternus MARSH. Amer. Journ. of Science 1869, p. 397.

SYNONYMIK

Die Synonymik der verschiedenen amerikanischen Genera und Species der Pythonomorphen ist bis jetzt nicht genügend aufgeklärt und eine Erörterung derselben ist für den, der das ganze Material in den amerikanischen Museen nicht gesehen hat, unmöglich, da die Beschreibungen der Genera und Species nicht vollständig genug sind, um ein genaues Bild zu geben.

Tabelle

In der nachstehenden Tabelle befindet sich eine kurz gefasste Diagnose von den bis jetzt festgestellten Gattungen der amerikanischen Pythonomorphen.

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[30] Nach Vollendung des Manuscriptes habe ich das Original von Prof. MARSH's *Baptosaurus* gesehen, und habe mich überzeugt, dass die Reste im Münchener Museum wirklich dem Genus *Baptosaurus* angehören.

Platecarpus	*Clidastes*	*Tylosaurus*
Halswirbel mit schwachem Zygosphen, starken Zygapophysen und gegliederten Hypapophysen.	Halswirbel mit starkem Zygosphen und Zygapophysen und gegliederten Hypapophysen.	Halswirbel mit Zygapophysen, sehr schwachem Zygosphen und gegliederten Hypapophysen.
Schwanzwirbel mit freien Haemapophysen.	Schwanzwirbel mit Haemapophysen, die mit den Centren verwachsen sind.	Schwanzwirbel mit freien Haemapophysen.
Basioccipitale oft durchbohrt. Hypapophysen nicht horizontal zusammengedrückt.	Hypapophysen des Basioccipitale seitlich nicht zusammengedrückt.	Hypapophysen des Basioccipitale seitlich zusammengedrückt.
Lappenartige Fortsätze des Ex-Occipitale die sich über die Vorderseite der Hypapophyse des Basioccipitale hinüber erstrecken, bis zum Unterende derselben reichend, dick und breit.	Lappenartige Fortsätze des Ex-Occipitale bis fast zum Unterende der Hypapophyse reichend, aber dünn und nicht sehr breit.	Lappenartige Fortsätze des Ex-Occipitale laterale sehr kurz, nicht mehr als zur halben Länge der Hypapophyse reichend.
Hintere Fortsätze des Basisphenoid kurz, nur wenig länger, als die vorderen.	Hintere Fortsätze des Basisphenoid ungefähr von der Länge der vorderen.	Hintere Fortsätze des Basisphenoid zwei Mal so lang wie die vorderen.
Parietale oben, vorn mit einem erhabenen Feld. Foramen parietale gross, fast an der Grenze zwischen Parietale und Frontale.	Parietale oben ganz eben. Foramen parietale klein, ziemlich entfernt von der Coronalsutur.	Oberseite des Parietale ganz eben. Foramen parietale an der Grenze zwischen Frontale und Parietale.
Hinterrand des Frontale eingebuchtet. Seitenränder über den Augenhöhlen ausgeschnitten. Mit Nebenspitzen.	Frontale sehr lang, meistens ohne Nebenspitzen. Ueber den Augenhöhlen ziemlich tief, am Hinterrand wenig ausgeschnitten.	Hinterrand des Frontale fast convex, Seitenränder nicht ausgeschnitten. Mit Nebenspitzen. Mit grossen, länglichen, vom Foramen parietale ausstrahlenden Gruben verziert.
Vordere Spitze des Postfrontale nicht in eine grosse Vertiefung, am Hinterende des Praefrontale eingepasst.	Vordere Spitze des Postfrontoorbitale durch eine ziemlich grosse Lücke vom Praefrontale entfernt.	Vordere Spitze des Postfrontale über das Hinterende des Praefrontale übergreifend und daselbst sich in eine grosse rinnenartige Vertiefung legend.
Quadratojugale mit kurzem, schmalem Oberflügel.	Quadratojugale, mit kurzem, schmalem Oberflügel.	Quadratojugale, Kopf etwas nach nach unten gebogen. Mit grossem, langem Oberflügel.

Platecarpus	*Clidastes*	*Tylosaurus*
Quadratum. Supracolumellar-Fortsatz lang, am Hinterende breit, Innenrand desselben fast gerade. Vorderrand oben schwach concav nach vorn. Flügel in der Mitte dünn.	Quadratum. Supracolumellar-Fortsatz am Ende breit, gerade abgestutzt. Länge wie bei *Tylosaurus*. Flügel in der Mitte sehr dick. Vorderrand oben eingebuchtet. Innenrand oben stark eingebuchtet.	Quadratum. Supracolumellar-Fortsatz spitz endigend, nicht länger als die Hälfte der Länge des Oberrandes zwischen Hakenspitze und Hinterecke. Innenrand der Oberseite etwas eingebogen. Vorderrand oben stark eingebuchtet. Innenecke desselben spitzig.
Praemaxillare. Stiel langsam sich nach hinten verjüngend bis zur Mitte der Nasenlöcher. Schnauze vorn breit, zuweilen vor dem ersten Paar Zähne eingekerbt.	Praemaxillare. Stiel mit Maxillare bis zum 6. Zahn in Berührung und sich dann rasch verjüngend. Schnauze ausgezogen und fast spitz endigend. Schnabelartige Verlängerung d. Schnauze, nicht länger als der Durchmesser der Basis des ersten Zahns.	Praemaxillare. Stiel bis zum 6. Zahn mit dem Maxillare in Contact, sich dann plötzlich verjüngend. Schnauze schnabelartig verlängert, rundlich, am Ende stumpf abgeschnitten, länger als der Durchmesser der Basis des ersten Zahnes, vor dem ersten Paar Zähne mit einem kleinen Wulst.
Maxillare. Bis zum dritten Zahn von den Ansatzflächen für das Praemaxillare abgeschnitten. Oberrand hinter dieser Stelle ziemlich tief concav. Mit 12 Zähnen.	Maxillare. Bis zum 6. Zahn von dem Praemaxillare schräg abgeschnitten. Mit 17 Zähnen.	Maxillare. Bis zum 5. oder 6. Zahn vom Praemaxillare-Stiel schräg abgeschnitten; mit 13 Zähnen.
Vomer. Aussenseite des Kopfes nicht punktirt.		Vomer. Kopf auf der Aussenseite stark punktirt.
Palatinum. Rinne zur Aufnahme des Maxillar-Randes sehr klein.	Palatinum. Haupttheil sehr lang.	Palatinum. Rinne zur Aufnahme des Maxillar-Randes breit.
Pterygoid. Bezahnter Theil etwas S-förmig; mit 10–12 Zähnen.	Pterygoid. Wenig S-förmig, mit 15 Zähnen.	Pterygoid. Wenig S-förmig. Mit 10–11 Zähnen.
Transversum. Innenast einspitzig, gewöhnlich etwas verdickt.		Transversum. Innenast zweispitzig, mässig dünn.
Mandibel. Vorderende des Dentale schmal, erster Zahn dicht am Vorderende; mit 12 Zähnen. Coronoideum nicht ganz halb so lang wie der Oberrand des Supraangulare vor der Gelenkpfanne, Hinterflügel desselben klein.	Mandibel. Vorderende des Dentale schmal, abgerundet; mit 18 Zähnen. Coronoideum sehr gross und mit grossem Flügel.	Mandibel. Dentale vorn um ungefähr die Länge des Durchmessers der Basis des ersten Zahnes unbezahnt, vorn breit, meistens gerade abgeschnitten, mit 13 Zähnen. Coronoideum wie bei *Platecarpus*.

Platecarpus	*Clidastes*	*Tylosaurus*
Bezahnung. Dentale 12; Maxillare 12; Praemaxillare 2:2; Pterygoid 10–12 Zähne. Kieferzähne aussen meistens stark facettirt, innen gestreift, rundlich bis comprimirt.	Bezahnung. Dentale 18; Maxillare 17; Praemaxillare 2:2; Pterygoid 15 Zähne. Kieferzähne rundlich bis comprimirt. Facettirung und Streifung schwach oder fehlend.	Bezahnung. Dentale 13; Maxillare 13; Praemaxillare 2:2; Pterygoid 10–11 Zähne. Kieferzähne mit rundlicher Basis, gegen die Spitze comprimirt. Innenseite stark gestreift.

Sironectes COPE. Wirbel mit starkem Zygosphen. Chevron-Bones mit den Wirbelcentren gelenkig verbunden.

Baptosaurus MARSH. Halswirbel sehr stark vertical zusammengedrückt, mit breiten nach unten gerichteten Diapophysen. Ohne Zygosphen. Articulare hinter der Gelenkpfanne des Quadratum steil ansteigend.

Mx. = Maxilla
Pmx. = Praemaxilla
D. = Dentale
Op. = Operculare
Ang. = Angulare
S.Ang. = Supraangulare
Art. = Articulare
K. = Coronoideum
Q. = Quadratum
Qu.J. = Quadratojugale
Sq. = Squamosum
Pa. = Parietale
Fr. = Frontale

Ptf. = Postfrontoorbitale
Jug. = Jugale
Prf. = Praefrontale
Na. = Nasalia
Pal. = Palatinum
Ptg. = Pterygoid
Pr. = Prooticum
Exo. = Exoccipitale
Bsph. = Basisphenoid
Ba. = Basioccipitale
Hy. = Hyoideum
Vo. = Vomer
Turb. = Turbinalia

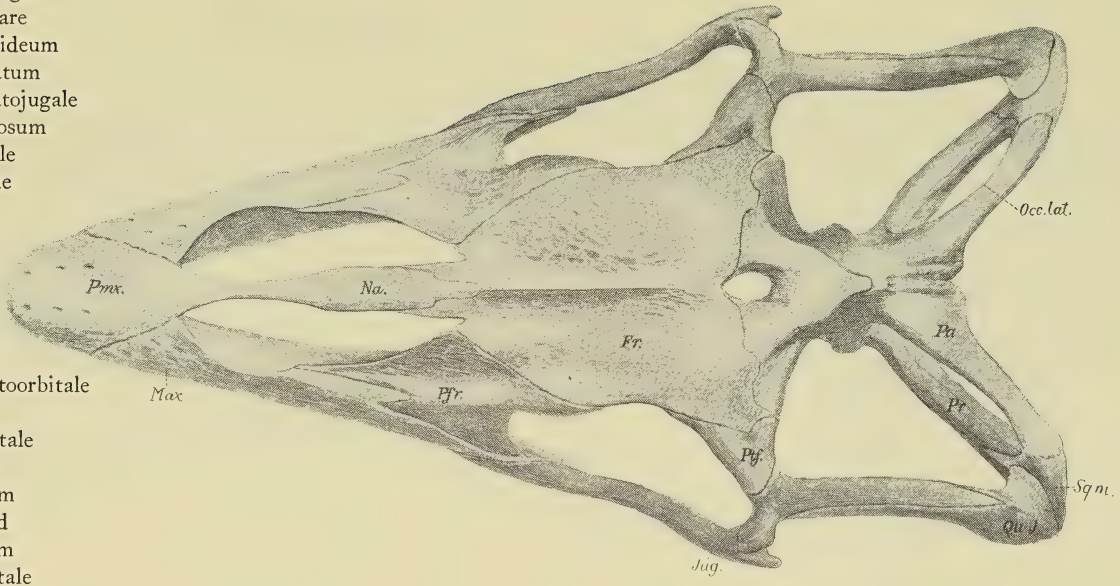


FIG. 1. *Platecarpus coryphaeus* COPE, Schädel von oben, .3 nat. Gr.

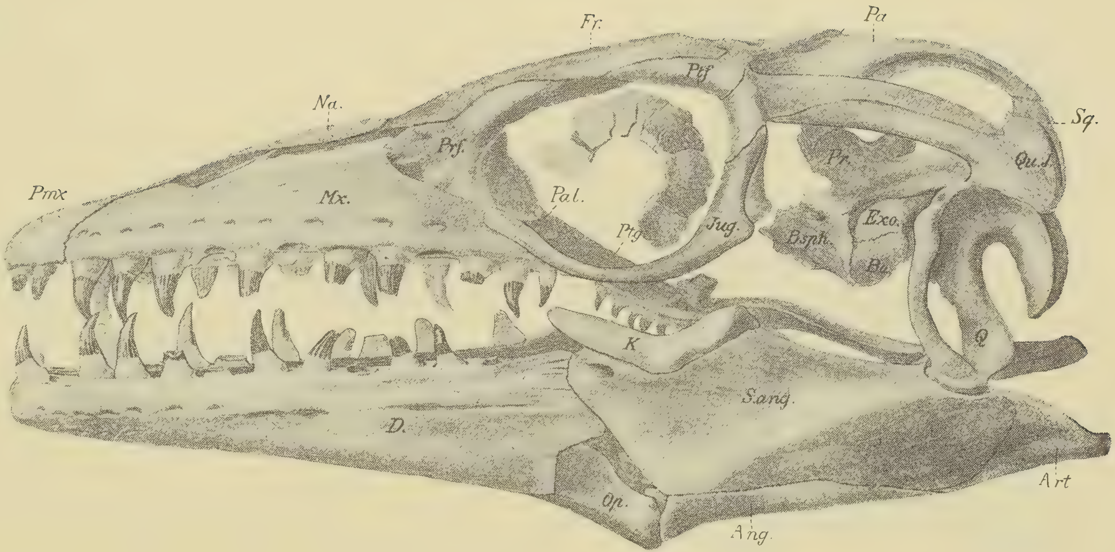

Fr.
Pa
Na.
Ptf
Sq.
Prf.
Pr.
Qu.J
Pmx
Mx.
Pal.
Ptg
Jug.
Exo.
Bsph.
Bo.
Q
K
S.ang.
D.
Art
Op.
Ang.

Fig. 2. *Platecarpus coryphaeus* Cope, Schädel von der Seite, .3 nat. Gr.
(For explanation of the lettering see plate I, fig. 1)

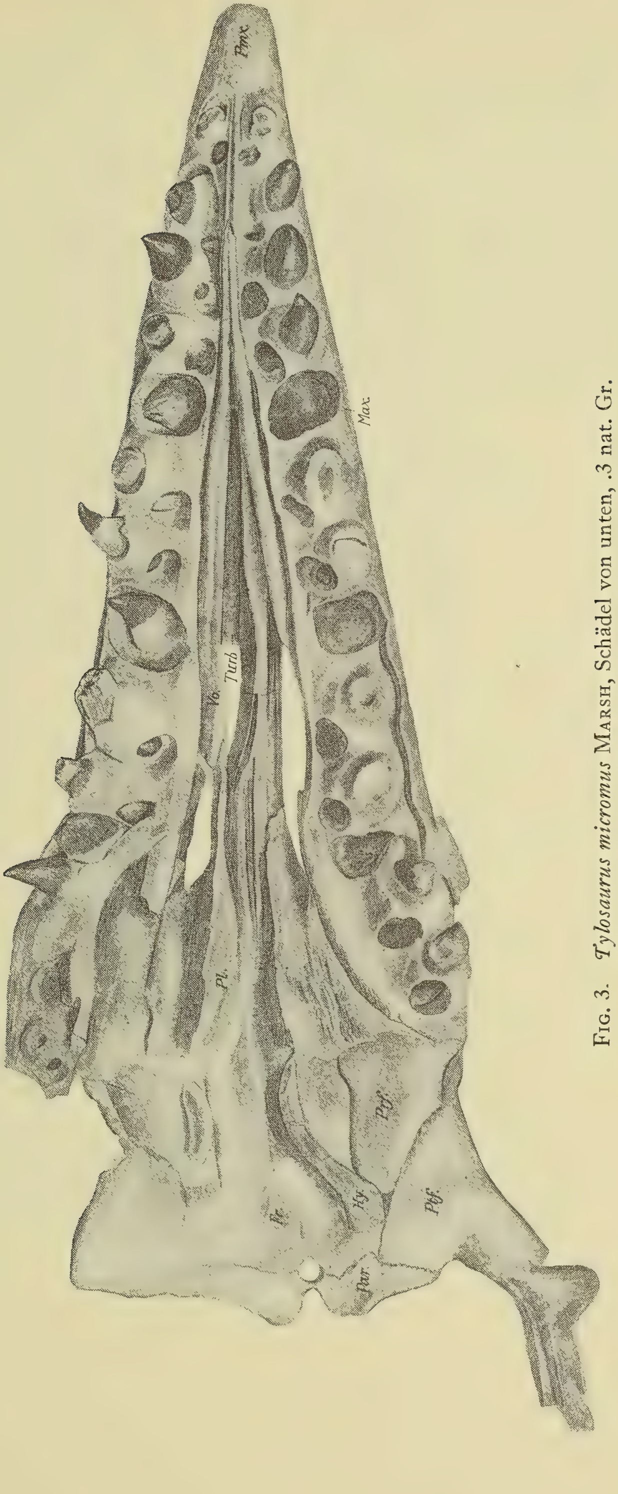

Pmx
Max
Vo.
Turb
Pl.
Prf.
Ptf.
Hy.
Fr.
Par.

FIG. 3. *Tylosaurus micromus* MARSH, Schädel von unten, .3 nat. Gr.
(For explanation of the lettering see plate I, fig. 1)

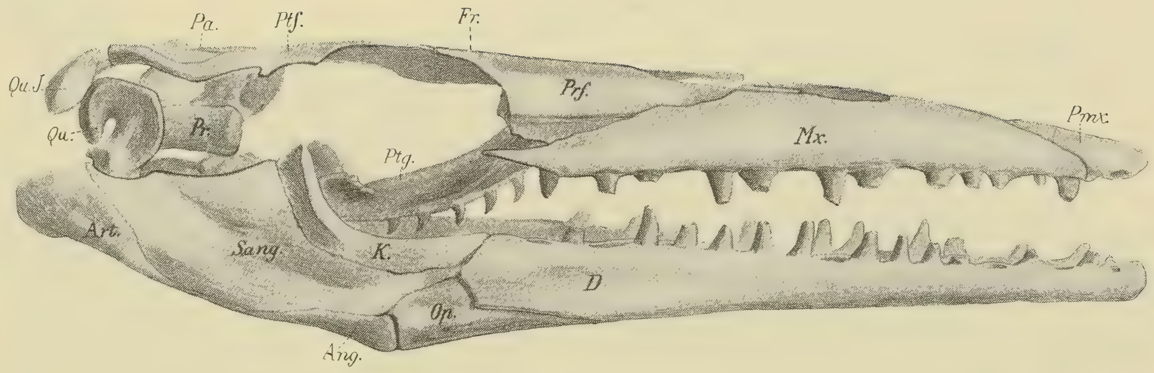
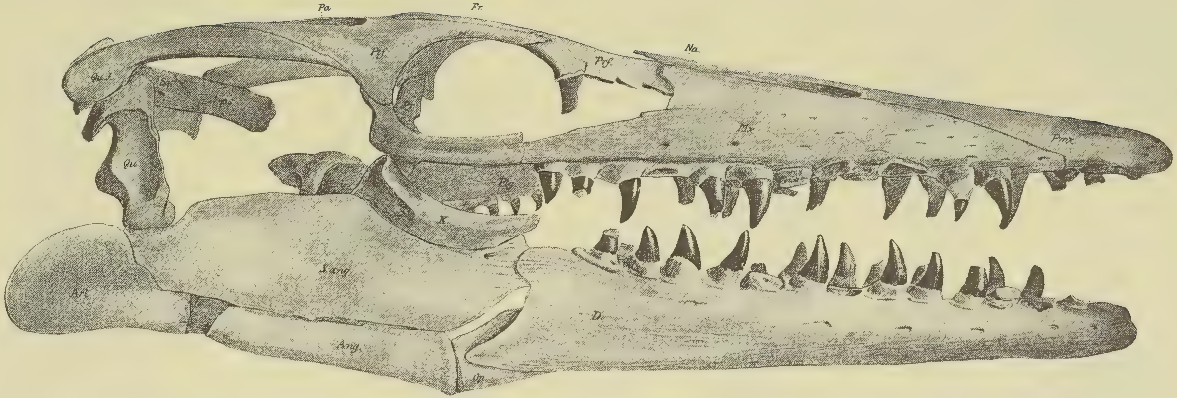

Pa.
Ptf.
Fr.
Qu.J.
Prf.
Pmx.
Qu.
Pr.
Mx.
Ptg.
Art.
Sang.
K.
D
Op.
Ang.

FIG. 4. *Clidastes velox* MARSH, Schädel von der Seite, .3 nat. Gr.
(For explanation of the lettering see plate I, fig. 1)


Pa
Fr.
Na.
Ptf.
Prf.
Qu.J.
Sq.
Pr.
Mx.
Pmx.
Qu.
Ptg.
K.
S.ang.
Art.
D.
Ang.
Op.

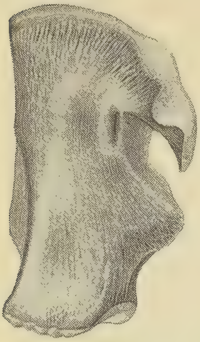
Tylosaurus proriger Cope. Schädel von der Seite, .13 natürliche Gr.

Pmx. = Praemaxilla
Mx. = Maxillare
D. = Dentale
Op. = Operculare
Ang. = Angulare
S.Ang. = Supraangulare
K. = Coronoideum

Art. = Articulare
Q. = Quadratum
Qu.J. = Quadratojugale
Ptf. = Postfrontoorbitalia
Fr. = Frontale
Na. = Nasalia
Prf. = Praefrontalia

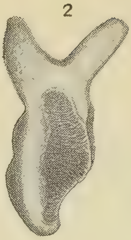
Ptg. = Pterygoid
Ju. = Jugale
Sq. = Squamosum
Pa. = Parietale
Ba. = Basioccipitale
Pr. = Prooticum

1



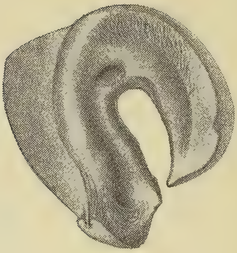
Rechtes Quadratum von *Tylosaurus proriger* Cope, von innen.

2



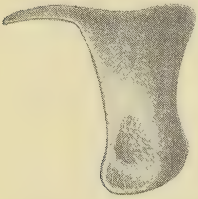
Rechtes Quadratum von *Tylosaurus proriger* Cope, von oben.

3



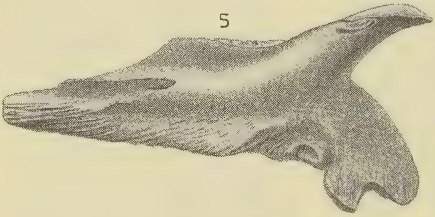
Rechtes Quadratum von *Platecarpus coryphaeus* Cope, von innen.

4



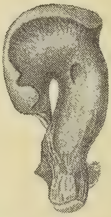
Rechtes Quadratum von *Platecarpus coryphaeus* Cope, von oben.

5



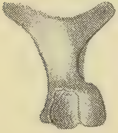
Linkes Praefrontale von *Platecarpus coryphaeus* Cope, von aussen.

6



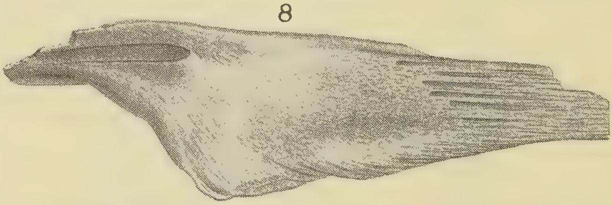
Linkes Quadratum von *Clidastes velox* Marsh, von innen.

7



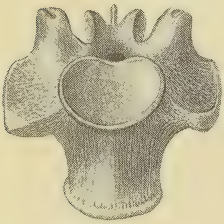
Linkes Quadratum von *Clidastes velox* Marsh, von oben.

8



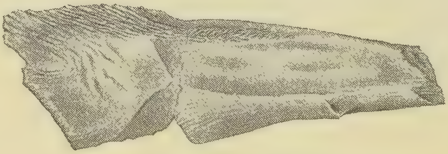
Rechtes Praefrontale von *Tylosaurus micromus* Marsh, von aussen.

9



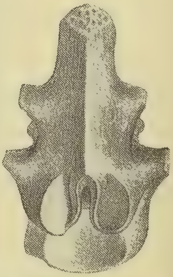
Dorsalwirbel von *Clidastes velox* Marsh, das Zygosphen zeigend.

10



Rechtes Praefrontale von *Clidastes velox* Marsh von oben.

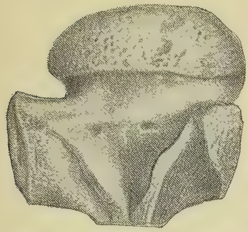
11



Halswirbel von *Platecarpus coryphaeus* Cope, das rudimentäre Zygosphen zeigend.

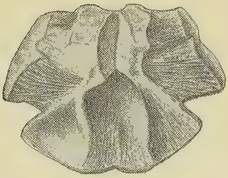
Alle Figuren $\frac{3}{8}$ nat. Gr.

1



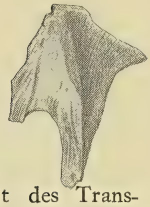
Basioccipitale von *Tylosaurus micromus* Marsh, von unten.

2



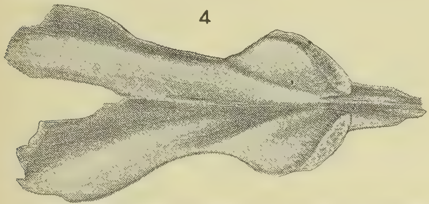
Basioccipitale von *Platecarpus coryphaeus* Cope, von oben.

3



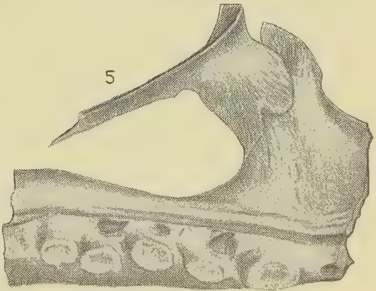
Innenast des Transversum von *Tylosaurus dyspelor* Cope, von oben.

4



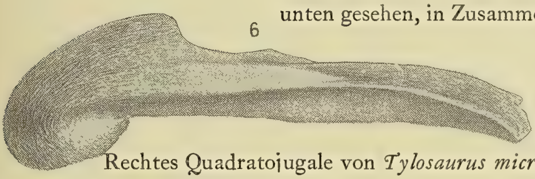
Basisphenoid von *Tylosaurus dyspelor* Cope, von unten.

5



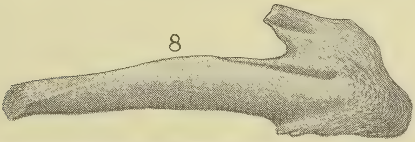
Linkes Transversum von *Tylosaurus micromus* Marsh, von unten gesehen, in Zusammenhang mit dem Pterygoid.

6



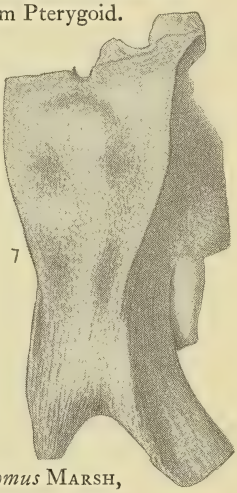
Rechtes Quadratojugale von *Tylosaurus micromus* Marsh, von aussen.

8



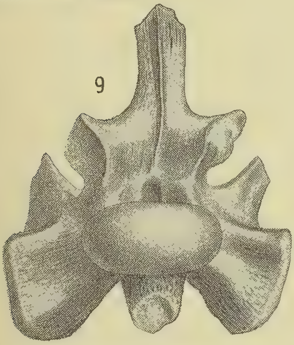
Linkes Quadratojugale von *Platecarpus coryphaeus* Cope, von aussen.

7



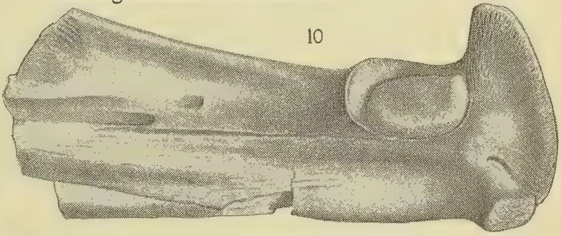
Parietale von *Tylosaurus micromus* Marsh, von oben. Die unteren Lappen sind seitwärts geschoben und sichtbar.

9



Halswirbel von *Baptosaurus onchognathus* nov. spec., von hinten.

10



Hinterende des rechten Unterkiefers von *Baptosaurus onchognathus* nov. spec.

Alle Figuren $\frac{3}{8}$ nat. Gr.

ON SOME REPTILIAN REMAINS FROM THE TRIASSIC OF NORTHERN CALIFORNIA

Although the Mesozoic of California is remarkably developed, both as regards thickness of section and richness of invertebrate faunas, it has so far appeared singularly barren of those characteristic and often abundant reptilian forms occurring in most Mesozoic rocks. Probably the only reptilian remains of this age found in California up to this time were collected in the summer of 1893 by Prof. Jas. Perrin Smith of Stanford University, in the Triassic of Shasta Co. Through the kindness of Prof. Smith it has recently been the writer's privilege to examine these specimens and prepare the following note.

The saurian remains, representing two individuals differing greatly in size, were found in the black Triassic limestone of Shasta Co., associated with a rich invertebrate fauna made up of such forms as *Arcestes*, *Trachyceras*, *Atractites*, *Aulacoceras* and *Tropites subbullatus*, all characteristically Triassic. The more exact stratigraphic relations of the horizon as determined by Prof. Smith place it in the upper portion of the Triassic.[1]

Both skeletons are very fragmentary and were so closely united with the matrix that in the case of the vertebræ successful preparation was almost impossible. The remains of the larger individual, consisting of eight consecutive vertebræ, a few fragments of ribs, and both coracoids, were imbedded in a loose slab about two feet square, and from the position of the parts present it might be inferred that they were in their natural relative positions. If this is the case the vertebræ would belong to the anterior part of the dorsal or posterior part of the cervical region. The rib fragments next the vertebræ and evidently belonging to them seem to be from the thorax. The *vertebræ*, Fig. 1, which resemble very much those of *Ichthyosaurus*, were very deeply bi-concave, possessed separated neurapophyses resting on a distinct facet on either side

American Journal of Science, ser. 3, vol. 50, no. 295, pp. 55–57, July 1895.

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[1] Journal of Geology, Vol. ii, No. 6, p. 607.

of the deep neural groove, and supported rather heavy single headed ribs. The centra are much shortened antero-posteriorly, measuring 34–38^{mm} long by 60^{mm} high and 70^{mm} broad. Those at the anterior end of the series are somewhat shorter than the others. The neurapophyses, as shown in the figure, were much thickened transversely by a broad rib running from the upper to near the lower end of the process. Zygapophyses were preserved on only one spinal process and seemed in this case to be small and weak. The *ribs* differ decidedly from those of *Ichthyosaurus*, articulating with one head only on the ample facets of the diapophyses and failing to show the external groove characteristic of many species of this genus.

1.

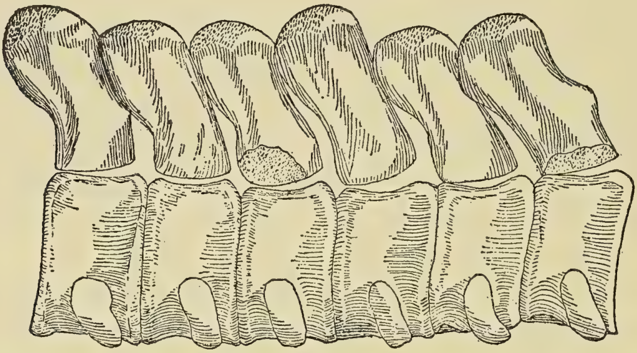

Fig. 1. Anterior dorsal (?) vertebræ of *Shastasaurus pacificus* gen. et sp. nov. One-third natural size.

2.

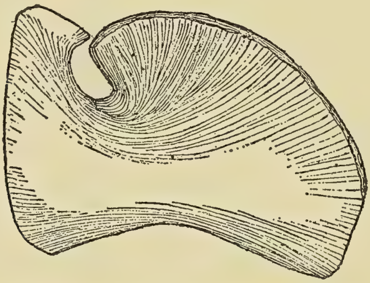

Fig. 2. Right coracoid of *Shastasaurus pacificus* from below. One-third natural size.

The strong and robust *coracoids*, one of which, Fig. 2, is perfectly preserved, were proximally much thickened and deeply notched on the anterior side. That they met on the median line, is shown by the sudden straightening of the distal margin shown in the figure. Judging from the small size of the surface of articulation with the scapula this element was small. The articular surface for the humerus being exceptionally large, this bone, as well as the whole fore-limb, probably partook of the robust character common in the anterior limbs of Enaliosaurs. The coracoids differ markedly from those of *Nothosaurus*, but approach the form of this element in some ichthyosaurian species.

Owing to paucity of material it is hardly possible to determine with certainty the exact affinities of the species described above, so much, however, is certain, viz: that its systematic position falls within the limits of the old order, *Enaliosauria*, which has perhaps not altogether outlived its usefulness. The majority of the characters, such as extreme shortness of centra, high degree of biconcavity of vertebræ, small zygapophyses, character of articulation of neurapophyses, and form of coracoid indicate ichthyosaurian affinities. Some of these characters, however, are also found occasionally in the *Sauropterygia*, while heavy, ungrooved, single headed ribs are characteristic of this order and do not occur in the *Ichthyosauria*. As no genus heretofore described contains this assemblage of characters the new generic and specific name *Shastasaurus pacificus* is proposed for this form.

The second and smaller individual is represented by about twenty-five vertebræ, mostly anterior caudals. As the whole series measures only 200^{mm} long the animal was many times smaller than *S. pacificus*. In the characters of the vertebræ alone there is nothing which would separate this species from *Ichthyosaurus*, but an ungrooved, single headed rib belonging to the anterior or middle dorsal region indicates shastasaurian affinities. This specimen probably represents a form different from that described above, but the material at hand is insufficient for specific characterization.

University of California, Berkley, May, 1895

TRIASSIC REPTILIA FROM NORTHERN CALIFORNIA

Triassic Reptilia from Northern California: John C. Merriam, Berkeley, Cal.

Reptilian remains were first discovered in northern California in 1893, when Professor James Perrin Smith obtained two short series of vertebræ and two arch bones in the Triassic limestones. These specimens were described by the writer in 1895, under the name of *Shastasaurus*, and were thought to belong to a form closely related to the Ichthyosauria, though they did not appear to find a place in any known genus. During the summer season of 1901 a quantity of new material was obtained from the original locality. The collection includes considerable parts of five skeletons, also numerous loose limb-bones, vertebræ, ribs, etc. Nearly all of the specimens belong to the genus *Shastasaurus*, of which there are several well-characterized species. Two nearly complete series of dorsal and cervical vertebræ show *Shastasaurus* to be characterized by possessing single-headed ribs on all of the vertebræ in this region excepting the anterior 8–9. In the cervicals the parapophysis is relatively small and in the anterior dorsal region it disappears entirely. As far back as the middle dorsals the articular surface of the diapophysis is confluent with that for the reception of the upper arches. The anterior and posterior limbs have not been found together, but are known from species having the same type of vertebræ and ribs. The anterior limb is ichthyosaurian in type, but the transverse diameter of the humerus is much greater than the longitudinal. The radius and ulna are very short and are separated by a considerable space. In the posterior limb the femur resembles that of *Ichthyosaurus*. The tibia and fibula are longer than in that genus and are separated by a wide cleft.

Abstract of paper presented at third annual meeting of Cordilleran Section, Geological Society of America, San Francisco, December 30 and 31, 1901. *Science*, n. s., vol. 15, no. 376, pp. 411–412, March 14, 1902.

The anterior arch is ichthyosaurian excepting the scapula which is very broad. The posterior arch is very different from that of *Ichthyosaurus*. The skull is not well known. The dentition resembles that of *Mixosaurus*. The forms of this genus represent a distinct group of the Ichthyosauria. In some respects they are generalized and resemble *Mixosaurus*, in the other characters they show specializations which separate them from the other members of the family.

TRIASSIC ICHTHYOPTERYGIA FROM CALIFORNIA AND NEVADA

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INTRODUCTION

IN THE spring of 1895, the writer received from Professor James Perrin Smith of Stanford University a number of vertebræ and limb bones collected by him in the Triassic of Shasta County, California. In the same year, these remains were described and figured under the name of *Shastasaurus pacificus* (Merriam,

University of California Publications, *Bulletin of the Department of Geology*, vol. 3, no. 4 pp. 63–108, pls. 5–16, June 1902.

1895). The genus was stated to have its closest affinities with the Ichthyosauria but to differ in some important particulars from all known forms in that group.

During the summer of 1901, the writer visited the Triassic areas of Shasta County in company with Professor Smith and a party of students from Stanford and California universities. On this expedition a considerable quantity of new material was obtained. In the fall of 1901, Miss A. M. Alexander generously contributed funds for another expedition into the Shasta region. Under the direction of Mr. H. W. Furlong, this party spent two months in the field and obtained some very valuable specimens.

In working up these collections, it was found necessary to compare the Californian material with that which had been described from the Triassic of Nevada by Dr. Joseph Leidy, and through the kindness of Dr. Charles R. Eastman the type specimens of Leidy's species were obtained for study from the Whitney collection at Harvard University. In examining them it was discovered that Leidy had overlooked the most important characters of the species which they represent. The writer has, therefore, included in this paper a redescription of the known Nevada forms.

Practically all of the saurian material that is known to have been collected in the Triassic of this coast has been brought together in preparing the following discussion. Forms which are not recognized as representatives of the Ichthyopterygia are reserved for description in a later paper.

For the present, two groups of species are recognized, those generally identical with *Shastasaurus*, from the upper Triassic of Northern California; and the middle Triassic forms from Nevada, which are all included in *Cymbospondylus* Leidy. These genera are probably closely related and form a well defined subdivision of the Ichthyopterygia. As yet but little is known concerning the structure of *Cymbospondylus*, while *Shastasaurus* is represented by specimens showing nearly all of the skeleton, so that the principal discussion of the structure and affinities of this group naturally falls in the description of the better known genus.

For the preparation of the drawings used in illustrating this paper, the writer is much indebted to Mr. Raymond Carter. The photographs were all taken by Mr. B. F. White.

FORMS FROM UPPER TRIASSIC OF NORTHERN CALIFORNIA, SHASTASAURUS GROUP

Occurrence

All of the saurian material which has so far been discovered in the Shasta region has been found in two limestone areas lying in the northern part of the county. Most of the specimens have been obtained from a large area between Squaw Creek and Pitt River, a few miles north of Winthrop Post Office. It was in this region that Professor Smith made the first discovery of saurian remains in 1893. A few fragmentary but interesting specimens have also been found in a small outcrop on the western slope of Bear Mountain, twenty miles northeast of Redding. Mr. O. B. Sherman of Bear Valley was the first to notice saurian bones at this locality.

The beds in which these remains occur have been described by Dr. H. W. Fairbanks[1] and Professor James Perrin Smith.[2] They are considered by Professor Smith as the equivalent in age of the Hosselkus limestone. The following extract from his paper cited above gives unquestionable evidence as to their age:

"The Hosselkus limestone may be conveniently divided into three divisions, the lowest of which is the *Trachyceras* beds, so called from the large number of that genus found at this horizon.

"These beds are about fifty feet thick, and are composed of rather hard, pure limestone, made up almost entirely of fossils; a large majority of all the Triassic species were taken from this horizon.

"The best collecting ground was found on the ridge between Squaw creek and Pitt river, about three miles northeast of Madison's ranch. The following fossils were collected at this locality:

Arpadites aff. A. *cinensis*, Mojsisovics.
Balatonites sp. group of B., Arietiformes.
Balatonites sp. group of B., Gemmati.
Polycyclus conf. *henseli*, Oppel.
Tirolites conf. *foilaceus*, Dittmar.
Trachyceras conf. *aon*, Muenster.
  " aff. *aonides*, Mojsisovics.
  " conf. *archelaus*, Laube.
  " aff. *armatum*, Muenster.
  " conf. *ladinum*, Mojsisovics.

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[1] Am. Geol. July, 1894, Vol. XIV, p. 27.

[2] Jour. Geol. Oct., 1894, Vol. II, p. 606.

Trachyceras conf. *hylactor*, Dittmar
“ sp. (like *Tirolites* in youth).
“ sp. (with fine costæ in youth, coarse in age).
Tropites subbullatus, Hauer.
“ sp. (with narrower coil than *T. subbulatus*).
“ sp. (with smooth narrow coil).
“ sp. (with rough narrow coil).
“ *saturnus*, Dittmar.
“ conf. *janus*, Dittmar.
Sagenites conf. *erinaceus*, Dittmar.
Halorites conf. *ramsaueri*, Gabb (not Hauer).
Eutomoceras conf. *sandlingense* Hauer.
“ sp.
Acrochordiceras sp.
Ptychites.
Nannites conf. *spurius*, Muenster.
Lecanites sp.
Arcestes conf. *californicus*, Hyatt.
Sageceras or *Beneckeia ?*
Nautilus triadicus, Mojsisovics.
“ sp.
Orthoceras sp.?
Atractites sp.
Aulacoceras sp.
Pecten sp.
Gervillia sp.
Halobia superba, Mojsisovics.
Posidonomya conf. *wengensis*, Wissmann.
Modiola sp.
Capulus sp.
Natica sp.
Rhynchonella conf. *solitaria*, Hyatt.
Terebratula sp.

“*The Atractites beds.*—These beds form the middle division of the Hosselkus limestone; they are very hard and siliceous, and while fossils are very numerous it is almost impossible to get out good specimens. The thickness of these beds is about 100 feet, but this is often seemingly increased by faulting. The rock is cut through in several directions by joints, and the weathering of the strata along these lines of weakness has given a rugged outline to the ridges, of which the *Atractites* beds usually form the top.

“At the locality three miles northeast of Madison’s ranch the following fossils were collected from this horizon:

Polycyclus conf. *henseli* Oppel.
Trachyceras (like *Tirolites* in youth).
    " conf. *aon*, Muenster.
Tropites subbullatus, Hauer.
    " sp. (with narrow coil).
    " sp. (with high-ribbed whorl).
    " *saturnus*, Dittmar.
Halorites conf. *ramsaueri*, Gabb.
Eutomoceras sandlengense, Hauer.
Eutomoceras sp.
Acrochordiceras sp.
Lecanites sp.
Arcestes, sp.
Nautilus triadicus, Mojsisovics.
Orthoceras.
Atractites (very common).
Aulacoceras sp. (rare).
Gervillia sp.
Modiola sp.
Margarita, sp.
Natica sp.
Rhynchonella conf. *solitaria*, Hyatt.
Nothosaurus sp.

"The bones referred to *Nothosaurus*[3] consist of a portion of the backbone about thirteen inches at length, together with several ribs, and fragments of other bones. Most of the species were found in much greater numbers and better preservation in the underlying *Trachyceras* beds, so that there is no great faunal distinction between the two horizons.

"*The Spiriferina beds.*—These beds are made up of about 50 feet of limestone like that of the *Atractites* beds, but harder and more siliceous. They contain numerous fossils, especially brachiopods, which, however, cannot be got out without dissolving the matrix. The most common fossil is a *Spiriferina*, or more probably, two species of this genus. Besides these are found:

Rhynchonella conf. *solitaria*, Hyatt
Terebratula sp.
Trachyceras sp.
Modiola sp.
Gervillia sp.
Pentacrinus sp.
Cidaris sp.

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[3] *Shastasaurus pacificus* Merriam.

"*Relations of the fauna of the Hosselkus Limestone.*—The fauna of the lower part of the Hosselkus limestone is undoubtedly that of the zone of *Tropites subbullatus* and *Trachyceras aon* of the Tyrolean Alps, that is of the lower Karnic. Several species are identical in the two regions, and many others very closely related. More than this, the stage of development of the ammonites is identical, which is quite as good a proof of similarity in horizon as identity of species."

The saurian bones are found in all three divisions of the Hosselkus limestone, but are best preserved and most common in the Atractites and Trachyceras beds.

Nearly all of the specimens are very firmly united with the matrix in which they are embedded. They are generally much like the rock in color and structure, so that in many cases it has been almost impossible to separate them from it or even to define their limits. In some specimens the difficulty in preparation has been increased by the presence of irregular bodies of siliceous material replacing the limestone. Fortunately, many of the bones are partly silicified, or a film of siliceous material has covered the walls of the canals and cavities, so that it has been possible to bring out their form and structure quite distinctly by the careful application of acids.

Practically the whole work of preparation was done by Mr. Eustace Furlong, to whom the writer is greatly indebted for his patient and skillful handling of this most refractory material.

CHARACTERISTICS OF SHASTASAURUS

The material serving as the foundation for this discussion includes considerable parts of seven individuals, together with many isolated bones and teeth. They represent nearly the whole of the skeleton, excepting the anterior part of the skull and the distal portions of the paddles.

All of the specimens seem to belong to one group, which is recognized as the genus *Shastasaurus*. Considerable differences among them are held to be of less than generic value. In addition to the type species, *S. pacificus*, five new forms *perrini*, *osmonti*, *alexandræ*, *careyi*, and *altispinus* have been recognized.

Vertebræ and Ribs.—Good material for the study of the vertebral column is furnished by a specimen of *osmonti* (Pls. 8 and 9) with which there is a good series of thirty-five vertebræ extending back from a point close to the head, with few if any interruptions. A specimen of *perrini* (Pls. 5 and 7) has an unbroken series of eighty vertebræ running from the anterior dorsal region to the posterior portion of the tail. In a specimen of *alexandræ* (Pl. 12) fourteen or fifteen vertebræ lie immediately behind the skull.

The centra are deeply biconcave in all regions of the column. The concave surface begins close to the periphery and slopes sharply but evenly to the middle. No case of normal perforation of the centrum has been discovered, though the partition between the concave surfaces is frequently very thin. In a single specimen it was possibly cut through by a minute canal. The upper arches are always free from the centra, and seem to have been separated from them by thick pads of cartilage. Excepting in the dorsals and anterior caudals of *perrini*, the longitudinal diameter of the centra is very much shorter than either the vertical or the transverse. In the vertebræ of *perrini* just mentioned the length may be two-thirds to three-fourths of the height.

In the cervical region the centra are somewhat broader than high. Through the greater part of the dorsal region these two dimensions are nearly equal and the cross-section circular or pear-shaped. In the caudal region the centra are laterally compressed and elliptical or pentagonal in cross-section.

The upper arches are slightly longer in the dorsal than in the cervical or caudal regions. Throughout the whole column they show a more or less pronounced tendency to the development of a heavy, lateral rib, produced by a sudden thickening of the median portion of the spine.

In the fifth and sixth cervicals of *alexandræ* the spines are very long and practically circular in cross-section near the summits. A loose cervical arch of *osmonti* shows a similar section. The anterior spines of the *perrini* specimen are somewhat thinner than those of *osmonti* but are probably not from the most anterior portion of the column. In what is taken to be an anterior dorsal arch of *osmonti* (Pl. 9, figs. 3 to 5) the antero-posterior diameter just above the posterior zygapophyses is 25 mm. and the thickness 13 mm. In an individual from the middle dorsal region the arch is 35 wide and 15 thick. In *perrini* the spines of the middle dorsals are much wider than in the anterior portion of the column, but continue to show the median thickening. In the type species, *pacificus* (Pl. 14, fig. 1), distinct ribbing appears on what are probably posterior dorsals. In *altispinus* (Pl. 15, figs. 3 and 4) the median or posterior dorsals seem to have higher and relatively thicker and narrower spines than in any other form. Excepting the blade-like anterior and posterior margins, their cross-sections are almost circular. Particular notice has been taken of this ribbing by Dames (1895, p. 1045) who calls attention to its presence in *Mixosaurus*. Either ribbing or a decided thickening of the arch would certainly seem to be a characteristic of Triassic Ichthyopterygia.

In the anterior dorsals and cervicals the pedicels of the upper arches are greatly extended laterally, so that they almost, if not quite, touch the ribs. This gives them an elongated triangular form at the base. The surfaces on the centrum, above which the upper arches rest, are excavated and considerably roughened. The excavation is extended laterally as a shallow groove upon the upper portion of the diapophysial ridge in the cervicals and anterior dorsals (Pl. 9, fig. 1). In the posterior dorsal region where the ribs are lower down on the side of the centrum, the pedicels lose their lateral projections.

On all excepting the posterior caudals, the arches are held together by well developed zygapophyses. In the cervicals they are large, strong, and wide. In the posterior dorsals they are weak but still effective, and are placed a little higher up on the spines. In all cases the facets are paired and separated by a narrow depression. They tend, however, to approach the same plane. In *osmonti* (Pl. 9, fig. 3) those in the anterior portion of the column if extended would ordinarily intersect at an angle between 150° and 160°, while in the middle or posterior dorsal region they practically come into the same plane. Their surfaces are slightly roughened, indicating the presence of considerable cartilage. They seem to be about intermediate in form between the type found in *Mixosaurus*, in which the facets cut each other at a fairly sharp angle, and that of the later Ichthyosaurs with the facets reduced, brought into the same plane, and united. The primitive form of zygapophysis is retained longest in the cervical and anterior dorsal vertebræ, or in those which have been least affected in the development of the powerful sculling tail of the Ichythyopterygia.

The mode of articulation of the dorsal ribs with the vertebrae furnishes one of the most important characters of this genus. In the anterior nine or ten vertebræ of *osmonti* (Pl. 8) and in those immediately behind the skull of *alexandræ* (Pl. 12), two distinct prominences with articular surfaces for the reception of the ribs are present. On the first and second vertebræ present in *osmonti*, the parapophysis has about half the vertical diameter of the diapophysis and is slightly anterior to it. Farther back on the column the parapophyses gradually decrease in size and were certainly not functional beyond the ninth or tenth. On the eleventh, there is a mere tubercle without an articular surface for the rib. The last trace is seen on the seventeenth, where a minute rudiment is present on one side only. In *alexandræ* the parapophysis of the fourth vertebra behind the skull is considerably less than half the length of the diapophysis, and the parapophysis of the tenth is so small that it was probably not functional.

The articular surfaces of the diapophyses are confluent with those for the reception of the upper arches from the anterior end of the column at least as far back as the thirty-fifth or thirty-seventh vertebra in *osmonti* (Pl. 8). In the specimen of *perrini* these two surfaces are confluent as far back as the twenty-seventh vertebra, where they are suddenly separated and the diapophysis moves to a lower position on the side of the centrum (Pl. 7, fig. 2). It is certain that some of the anterior vertebræ belonging to this specimen are absent. If they were all present, the point in the vertebral column at which the lowering of the diapophyses takes place would be close to the thirty-fifth vertebra, as in *osmonti*. In the posterior dorsal region the diapophyses are low down on the centra and remain in that position on the anterior caudals, but rise again slightly on the middle portion of the tail.

Compared with the height and length of the centrum, the diapophyses of the dorsals are longer and narrower than those of the cervicals. In *osmonti* the centrum of the first vertebra has a height of 39 mm., the diapophysis a height of 20 mm. In the thirty-fifth, the corresponding dimensions are 73 and 50.

On those vertebræ from which the parapophysis is disappearing, a slight constriction may be seen about the middle of the diapophysial ridge, and from this point the lower extremity swings forward to the anterior margin of the centrum. This character becomes more strongly marked toward the middle of the dorsal series (Pl. 8, fig. 5).

Corresponding to the form of the vertebrae, the cervical *ribs*

(Pl. 12) possess a large tuberculum and a small capitulum, the latter disappearing with the parapophyses. The two surfaces of articulation are separated by a notch corresponding to the depression between the di- and parapophyses of the centrum. Numerous ribs associated with the anterior dorsals of *perrini* and *osmonti* show no trace of the capitulum (Pl. 7, fig. 4 and Pl. 9, fig. 6). In the middle and anterior dorsals, the rib-head exhibits variation in form corresponding in a manner to that already described as occurring in the diapophyses. Though the heads are of approximately the size and form of the diapophysial surfaces, they cannot be closely fitted to them, as the middle of each face is more prominent than the superior and inferior ends, and when the lower portions of the opposed surfaces are in contact, the upper ends are separated by a considerable cleft (Pl. 15, fig. 6). That the upper portions of the opposite surfaces were normally not so near together as the lower is indicated by the impossible position taken by the rib when they are brought together, the shaft being then directed upward instead of downward. Their roughness, as compared with the lower surfaces, shows that there was more cartilage between them. It has already been noted that the lateral extension of the depression beneath the pedicel of the upper arch may stretch over the upper portion of the diapophysis. In the cervicals this groove is short and covered by the spine-like, lateral projection of the pedicel. In the middle dorsals, where the pedicels are not greatly expanded, the groove is even longer than in the cervicals and extends into the roughened upper surface of the diapophysis, where it is opposed to the rib-head (Pl. 8, fig. 5). The roughened and grooved upper surface of the diapophysis was evidently not a surface of direct articulation, but was covered by cartilage which connected it with the upper portion of the rib-head, while the smoother lower surface articulated almost directly with the portion of the rib opposite it.

As is apparent, the whole plan of rib attachment through the greater part of the dorsal region is quite different from that of the typical Ichthyosauria. In *Ichthyosaurus* the diapophysis and parapophysis are both present, are quite distinct, and are of approximately equal size as far back in the column as the posterior dorsal region, where they unite. Also, the articular surfaces of the diapophyses which are confluent with the neurapophysial surfaces in the cervical region, as in *Shastasaurus*, become separated from them at about the fourteenth or fifteenth vertebra instead of at the thirty-fifth or a later one. In *Shastasaurus* true double articulation is found in only a few of the most anterior vertebræ, and even there the parapophysis is relatively very small. The loss of the lower articular surface has been compensated for in the dorsal region, next the lungs, by elongation of the diapophysis and development of the method of attachment of the ribs just described. This permits a rocking movement of the ribs on the vertebræ, such as would be advantageous in inhalation by marine, air-breathing animals expanding the lungs considerably both at the beginning and the end of a period of long-continued submergence.

Short, robust ribs are seen in *alexandræ* close to the first vertebræ, and similar ones are associated with the anterior cervicals of *osmonti*. Toward the anterior dorsal region they elongate rapidly. In the posterior dorsal region they are shorter and heavier. Well developed diapophyses are present in the middle caudals in *perrini* (Pl. 5, fig. 1), but no ribs from this region have been uncovered. Contrary to the original description, the rib-shaft is usually grooved on both anterior and posterior sides (Pl. 5, fig. 1). This is most noticeable in the dorsal ribs, on which the grooves may be very deep. On the fragments of posterior dorsal ribs described with the type of the genus the grooves are not well marked. Both grooves begin close to the superior side of the shaft near the head and run out beyond the middle of its length. Excepting the head, the proximal half of the rib is narrow and rounded below. A broad, flat superior surface is bounded by the anterior and posterior grooves. The distal portion is almost circular in cross-section. The rib-head is rather sharply twisted from the plane of the flattened proximal portion of the shaft so that the upper portion is turned backward. This is so pronounced in the middle dorsal region of *perrini* that the plane of the rib-head is turned almost eighty degrees from that of the shaft (Pl. 7, fig. 4).

Associated with the distal ends of the dorsal ribs of *osmonti*, there are on one slab a large number of rib-like bodies very much smaller than the true ribs. Though it has not been possible to make out their form definitely, they appear to vary in shape somewhat, and almost certainly represent the several elements of a series of *abdominal ribs*. In *perrini* also, a number of fragments of very small ribs under the trunk may represent abdominal ribs.

Evidence of the existence of *intercentra* is found on the first three known cervicals of *osmonti* (Pl. 8, fig. 1), and the first four of *alexandræ*. A prominent apophysis on the middle of the lower side of the first cervical present in *osmonti* shows an anterior and a posterior facet, each extending to the intervertebral articular surface of the centrum. Although somewhat broken, the anterior facet appears to be larger than the posterior. On the second vertebra the inferior apophysis is situated on the anterior half of the centrum and possesses a large anterior facet similar in form but smaller than that on the rear of the vertebra in front of it. The posterior border of the second cervical is slightly elevated, as is also the anterior border of the third, and a small ossicle may have been situated between them. A small bone found with the anterior cervicals has the form and dimensions required for the intercentrum in front of the first vertebra and probably represents that element.

The facets for the reception of the intercentra on the first cervical in this series are much like those figured by Owen[4] for the second vertebra of *Ichthyosaurus longifrons*. It is, however, very doubtful whether the most anterior vertebra here is either atlas or axis, as the anterior end of the centrum presents a deep concavity similar to that in all the subsequent vertebræ, and entirely unlike either the anterior or posterior face of the atlas or the anterior face of the axis in *Ichthyosaurus*, as described by Owen. On the other hand, the small size of the vertebra, as compared with those behind it, and the rapid decrease in the size of the intercentra posteriorly indicate that the first centrum is probably not far removed from the skull. In *alexandræ* there is evidence of the existence of intercentra, at least as far back as the fourth cervical. It is pretty clear that there were more cervical intercentra in *Shastasaurus* than in *Ichthyosaurus*, as the last intercentrum in *Ichthyosaurus* is between the axis and the third vertebra.

Through a large part of the caudal region *hæmapophyses* are well developed. Unlike the lower arches of *Ichthyosaurus*, their inferior extremities unite to form long spines, or in other words, produce Y-shaped chevron bones (Pl. 5, fig. 1, and Pl. 7, fig. 3). In *perrini* the spinous portion of the arch may be double the length of the pedicels. The articulation of the lower arches is intervertebral, and pairs of small facets are developed on the adjoining posterior and anterior margins of the centra with which they are in contact.

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[4] Liassic Reptilia. Pl. 23, fig. 5.

The specimen of *perrini* shows the greater portion of the caudal region well preserved, and furnishes some interesting evidence concerning the character of the tail fin. The middle portion of the tail seems to be somewhat wider or higher than that of *Ichthyosaurus*, owing to the length of the hæmal spines, and was, consequently, more effective as a sculling organ. As is shown in Plate 5, fig. 1, the posterior portion of the caudal series is quite sharply deflexed, and evidently extended into the lower lobe of a fin like that now known to have existed in *Ichthyosaurus*. The bend in the caudal series is present at the place where it occurs in *Ichthyosaurus*, and as other portions of the vertebral column have not suffered much disturbance, it is probably due to normal curvature in the vertebral column of the living animal.

Arches.—The pectoral girdle of *Shastasaurus* is represented by a nearly complete arch in a specimen of *alexandræ* (Pl. 12) and the greater portion of a girdle belonging to *osmonti* (Pl. 10, fig. 1). Both specimens show this arch to be formed essentially as in *Ichthyosaurus*. In the specimen of *alexandræ* the arch lies on the top of the partly inverted cervical vertebræ. The left scapula and coracoid are brought into the same plane, while on the right side the scapula was doubled under the coracoid. The distal ends of the coracoids almost touch, and the left clavicle lies in front of the coracoid on that side. Being very slightly disturbed and above the partly inverted vertebræ, it is evident that it is the inferior surfaces of the arch bones that are exposed. As the superior side of the skull is uppermost, the body probably first lay on its side, and, in crushing down, the head turned slightly, coming into a horizontal position.

From this specimen the mutual relations of all of the arch bones can be made out with absolute definiteness. In the specimens of *osmonti* the elements, although not advantageously placed for study, were associated with the anterior limbs and cervical vertebræ and certainly belong to one individual.

The *coracoids* are quite different from the element figured with the original description of the genus. The bone which the author and others[5] supposed to be the coracoid has little in common with that element, though it shows some resemblance to the scapula. As will be shown later, it does not come from the pectoral arch at all, but probably belongs to the pelvic girdle. The coracoid of *alexandræ* resembles that of *Ichthyosaurus communis* somewhat, but is not so much expanded distally. In *osmonti* it is still narrower. It is very thick and heavy in both species, particularly so in *osmonti*, in which the distal end is 71 mm. thick, the greatest length of the bone being 150 mm.

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[5] Dames, Fraas. See Dames 1895, p. 1049.

The *scapula* has a broad triangular base (Pl. 10, fig. 5), on which is a large surface of articulation for the reception of the humerus, and a much smaller one on the anterior side where it rested against the coracoid. The thinner distal end is much expanded, and turns downward and forward, forming a sharp hook. It is quite different from that of any Ichthyopterygian previously known to the writer, but is somewhat similar to that of the Pythonomorpha. Its great distal expansion and anterior hook are distinguishing characters. It is not so large as the coracoid, but has about the same relative dimensions as in *Ichthyosaurus*.

A nearly perfect *clavicle* in the specimen of *alexandræ* is a long and rather slender bone with a very deep groove on the end next to the median line of the body. Along this depression it probably fitted over the transverse bar of an *episternum*. This latter bone is not well shown in any specimen, but is possibly represented in *alexandræ* by a fragment which looks like the left end of the transverse bar.

The complete *pelvic arch* is known only from *perrini*, where all of the elements from both sides are preserved (Pl. 5, and Pl. 6, fig. 1). In this specimen the bones referred to the pelvic region and the posterior limbs lie immediately in front of the first chevron-bearing caudals. That they have not wandered back from the pectoral region is shown by the fact that a considerable portion of an arch bone, probably a coracoid, much larger than any of those in question, is present immediately below the anterior dorsals; while the femurs and the whole six elements of the pelvic girdle are accounted for.

All three of the bones of the arch of *perrini* are so unlike anything which the writer has found referred to *Ichthyosaurus* that it has been necessary first to discover whether their position in the matrix can furnish a clew to their normal place in the arch. As the skeleton is resting on its left side, it is probable that the arch and limb bones on that side were next the sea bottom and immediately covered by the body, and would be subject to less disturbance than the corresponding elements of the upper or right side. The latter would be separated by a large mass of flesh from the sea floor, and in settling down after the body had decomposed might easily have been separated or moved out of their natural order. As the arch bones lie on the slab, one of them, *Isl*, is covered by a femur, another, *Pl*, seems to have had ribs lapping over it, and a third, *Il*, is partly covered by *Isr*. These three bones seem to have been on the lower side of the body. They are, moreover, grouped about the head of the femur *Fl* in such a way as they might be if they belonged with it. The other three bones are grouped with the corresponding ends near each other. Of these elements *Pl* and *Pr* are anterior to *Isl* and *Isr*. *Il* is nearer the vertebral column than the others from that side, and is probably the *ilium*. *Ir* does not occupy the same relative position, but may be displaced. *Pl* and *Pr* may be considered tentatively as the *pubic bones*, *Isl* and *Isr* as the *ischia*.

In comparing these elements with those of other swimming saurians, the supposed pubes and ischia are found to show some resemblance to those of *Plesiosaurus* and *Cimoliosaurus* and also to *Palaeohatteria*, though their positions are reversed. The elements which have been considered as the ilia are unlike any bone of the Ichthyosaurian or Plesiosaurian pelvis that has been accessible for comparison. An approach in form would be found in an inverted pubis of *Ichthyosaurus*, the ilium of the later Plesiosauria, or in the most common form of ischium of the Pythonomorpha. From all of these it differs so much that the writer has been unable to do better than depend for tentative determination upon their present position in the matrix, as previously stated. As careful a preparation as can be made of the proximal ends of the pelvic elements of *perrini* fails to show definitely more than a single articular surface, excepting in the ilium; so that it has not been possible to ascertain how they could be fitted together to receive the head of the femur. In what is considered as the pubis in *pacificus* (Pl. 14, fig. 2), a small articular surface seems to be present just below the hook, and on this the ischium may have been received.

This arch, as it is supposed to have been constructed, would bear a greater resemblance to that of the Plesiosauria than to any known relative of the Ichthyosaurs. It is so different from that of *Ichthyosaurus* that no doubt can exist as to this genus representing a separate line of descent. The arch of the known Jurassic forms could hardly be derived from it.

To the pubis of *perrini* the supposed coracoid of *pacificus* (Pl. 14, fig. 2), the type of the genus, shows a stronger resemblance than it does to any bone of the pectoral girdle, and inasmuch as it was associated with posterior dorsal vertebræ, it may be considered as representing that element. Particularly in the form of the proximal end it differs from both coracoid and scapula and resembles the pubis (text fig. 1, p. 103). In this connection it may be noted that the writer's association of the posterior dorsal vertebræ with the supposed coracoid, as doubtful anterior dorsals, was not without reason. His first opinion regarding the vertebræ was that they were anterior caudals, but the evidence in favor of their belonging with the undisturbed supposed coracoids was so strong that he accepted as a possibility the occurrence of a single articulation of the rib low down on the centrum. This belief was strengthened by the discovery of long single-headed ribs.

Extremities.—The *anterior limbs* are best represented in the specimen of *osmonti* (Pl. 10, fig. 1, and Pl. 11). With this there were found the right humerus, radius, ulna, radiale, and a fifth bone that may be an intermedium; and from the left side the humerus, radius, radiale, and a phalanx. The elements that are considered as belonging to the right limb were found together and in their natural positions in a small slab at the foot of the bluff. Close to them was what is known by comparison with *alexandræ* to be the right scapula. The proximal end of the right coracoid was exposed in the face of the cliff near by. The left coracoid was buried in the limestone just below the right, and the left humerus lay with its proximal extremity next that of the coracoid.

The *humerus* of this form, instead of being more slender than that of the later genera, as one would conjecture, is remarkably short and broad. Measurements of the right and left elements of the specimens of *osmonti* give the greatest length, taken from a point between the radius and ulna, as 170 mm. The greatest transverse diameter across the proximal end is 174 mm., and across the distal extremity approximately 180 mm. The least diameter, measured across from a deep, narrow notch on the anterior side to a broader posterior emargination, is 136 mm. As nearly as the writer has been able to determine, this is the shortest propodial segment known in the limb of an Ichthyopterygian form.

The anterior notch, to which attention has just been called, reminds one of those found in the radius of the longipinnate Ichthyosauria, and in other elements belonging to the middle portion of the limbs of both longipinnate and latipinnate forms. Lydekker[6] suggests that in these cases "were it not for the difficulty of explaining the presence of the same feature in the carpals and tarsals the notch in the anterior border of the radiale, tibiale, and phalangeals, might be regarded as the last trace of the shaft of a 'long bone.' . . ." In *osmonti* this notch is very narrow. In a portion of a much less robust humerus with the specimen of *alexandræ* (Pl. 12) it is much wider. The greatly shortened humerus of *Shastasaurus* presents almost exactly the conditions which Lydekker supposed necessary for the development of a notch, and its occurrence here tends to strengthen his theory.

The proximal end of the humerus is very convex, the cartilaginous portion extending far around both anteriorly and posteriorly. It is greatly thickened on the inferior or posterior face by a prominent ridge, extending three-fourths the length of the bone, and giving to this end a thickness of about 85 mm. The prominence is like the proximal end of the pectoral ridge of the Mosasaurian genus *Platecarpus*. The upper surface immediately opposite the proximal end of the inferior ridge shows a considerable excavation, which is bounded by a faint ridge in front and a broad, prominent elevation behind. The ulnar corner of the upper side is separated from the remaining surface by a well-marked groove, running from the posterior emargination to the posterior end of the radial border. The radial border is considerably longer than the ulnar and is slightly thicker excepting the posterior portion of the latter, which is added to by a prominence on the distal end of the upper surface.

The *radius* is a quadrate element, somewhat wider than long (width 110–115 mm., length 95). The proximal margin is nearly straight, the distal slightly convex, the posterior concave, and the anterior is marked by a deep, narrow notch, like that in the longipinnate Ichthyosauria. The *ulna* is considerably smaller than the radius in all of its dimensions (length 71 mm., width 85) and runs out to a comparatively thin edge on its posterior border. Its proximal margin is nearly straight, the small portion of the distal edge present is convex, the posterior side is also convex. The anterior border is slightly concave.

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[6] Catalogue of Fossil Reptilia and Amphibia in Brit. Mus. Part ii. p. 70.

The form of the adjacent margins of the radius and ulna shows that they must have been separated by a considerable cleft. Their positions with reference to the humerus, causing them to diverge distally, would probably increase the distance, so that there would be quite a wide space between them.

The *radiale* is somewhat larger than the ulna and might have been mistaken for it, had not their positions in the matrix been such as to preclude the possibility of such a confusion. The lower end of the bone is broken off, but as the break is evidently below the middle the absence of a notch on the portion present may be taken to indicate that the anterior margin was entire, since the emargination always occurs in the middle. If notching were caused by shortening of the shaft, as suggested by Lydekker, it could easily be present in the radius without having developed in the carpus.

Resting in the angle between the distal ends of the radius and ulna and the proximal extremity of the radiale was an elliptical ossicle, which possibly represents the *intermedium*. The border is deeply concave and was evidently surrounded by a thick layer of cartilage. A careful examination of the adjacent angles of the radius and ulna reveals no sign of a facet for contact with an intermedium. The posterior, distal corner of the radius is sharply angular, and the adjacent corner of the ulna is only slightly rounded, while the surfaces of both have been thickly covered with cartilage. The intermedium evidently did not fit closely between the radius and the ulna, but lay near them in a thick plate of cartilage. The form and position of the ossicle just described are such as would be found in the intermedium, and it will be considered as representing that element. The dimensions are about what one would expect it to possess (long diameter 50 mm., short diameter 42, thickness 23).

Two small ossicles, one of which probably represents a *phalanx*, were found mingled with the cervical vertebræ and ribs. One of them is similar to the element which has been considered as an intermedium, but is slightly shorter and about one-half as thick. It may be either a distal carpal or a phalanx.

On the other bone the proximal and distal ends are thickened and convex. One lateral margin is convex, the other deeply concave and considerably thinned. The length is 40 mm., the width 50, the thickness at the ends 20, and in the middle 14. The thinness of the middle portion and the concavity of one margin in this element may indicate the remnant of a shaft of a phalanx with thickened posterior margin and ends. This bone is possibly a part of one of the elements at the back of the skull.

The *hind limbs* are known only from the *perrini* specimen, with which there are present both femurs, a tibia, a fibula, and four small ossicles of doubtful relationships (Pl. 6). The tibia and fibula are associated with one of the femurs in such a way that there can be no doubt as to their relation to it. Two of the small bones may also belong with this limb. The other two and the second femur are not definitely connected with any of the other limb bones.

Compared with the humerus of *osmonti* and *alexandræ* the *femur* is relatively slender. Its length, 55 mm., slightly exceeds its greatest transverse diameter, which is found at the distal extremity. The shaft is considerably contracted in the middle, where its width is only a little more than half of its length. The expanded and flattened distal and proximal ends are twisted away from each other so that their long diameters intersect at an angle of about sixty degrees. The fibular facet is only about sixty per cent as long as the tibial, and is inclined about thirty to forty degrees away from the plane of the latter.

The larger of the elements next the distal end of the femur has been considered as probably the *tibia.* Its length is almost the same as its greatest width. The anterior border shows a shallow median notch. The posterior margin has suffered considerably from weathering, and it is not possible to determine its outline with absolute definiteness. As it now appears, this side is concave, and, judging from the structure of the bone, it was so originally.

The *fibula* is better preserved than the tibia, and little doubt can exist as to its original form. The distal end is considerably wider than the proximal. The well-preserved posterior margin is deeply concave. The anterior side has suffered considerably, but appears to have had much the same form as the posterior edge. Its length is the same as that of the tibia, but it is a much slenderer bone. Its width at the proximal end is less than two-thirds that of the tibia, the shaft is also much narrower. The distal end is almost as wide as the corresponding part of the tibia in its present weathered condition. Although the distal extremities of the tibia and fibula may have been in contact, there can be little doubt concerning the existence of a gap between their middle or shaft portions.

A portion of a small ossicle which originally lay between the distal ends of the tibia and fibula may have been the *intermedium*, or was possibly some other carpal or a phalanx. Another, which is between the anterior proximal corner of the tibia and the femur, is probably a loose *phalanx*, belonging with two seen a short distance in front. This element might possibly be considered as a pre-tibial ossicle, but the space into which it seems to fit would be largely closed up if the tibia were in its normal position. As the tibia now lies, it is moved a little to the rear. It would also be possible to make this a post-fibular ossicle like that seen in some Plesiosauria and Ichthyosauria, if this were considered the posterior side of the limb. It should, perhaps, be stated that if both the limbs and the arches were considered as reversed, or facing backward in the slab, they would come near to agreement with the general plan of Plesiosaurian posterior limbs and arches.

Judging from a comparison of the limbs with the middle dorsal vertebræ, it would appear that the posterior limbs were smaller and less specialized than the anterior.

Skull.—The posterior half of a cranium belonging to an undoubted representative of *Shastasaurus* was found with the type specimen of *alexandræ* (Pls. 12 and 13). This skull is typically Ichthyosaurian in nearly every particular. The small frontals are overlapped anteriorly by very large nasals. The superior portions of the parietals form a narrow ridge in which is a parietal foramen. The orbit is of enormous size, and the structure of its bony rim, as also that of the single temporal arch, is similar to that in *Ichthyosaurus*. The form of the jugal, lachrymal, and the prefrontal, is essentially as in *Ichthyosaurus*. The postfrontal meets the prefrontal above the middle of the orbit and considerably in advance of the temporal opening. The upper portion of the postorbital extends backward beneath the supratemporal and squamosal, which are partly broken away from this specimen. The quadratojugal is missing or moved from its natural position. The quadrate is of the Ichthyosaurian type. The end of the maxillary is present but is unfortunately broken off behind the posterior teeth. The otic bones, the supraoccipitals, and the lateral occipitals could be only partly exposed and their relations cannot be definitely determined. Sclerotic plates like those of *Ichthyosaurus* appear in both orbits.

On the lower side of the cranium the pterygoids and palatines have been well exposed and are similar to these elements in *Ichthyosaurus longifrons*, as figured by Owen. Portions of what are probably the basioccipital and basisphenoid and one of the quadrates are also shown. Close to the pterygoids there is present on each side a long rod-like bone, representing the thyrohyal of Owen, such as has been described by him from *I. tenuirostris*. Considerable portions of both rami of the mandible are present. The break at the anterior end of the left ramus shows the dentary, splenial, supra-angular, and angular. The splenial extends the whole height of the jaw at this point. The portion of the dentary shown is the thin posterior end supported by the supra-angular. The angular is hidden on the outside by the overlapping supra-angular. Toward the posterior end of both rami the angular is seen resting below the supra-angular. The sutures between these two elements are fairly well defined along the greater part of their contact, but are unfortunately obscured at several points. On the broken posterior portion of the right ramus there is visible the cross-section of a small bone, which may represent the coronoid. No trace of it is seen on the inner side of the left ramus; it is, however, possible that the angular has slipped over it, or that it has been destroyed in preparation. Concerning the form of the articular little can be said, as the region in which it should occur is very poorly preserved. Judging from the form of this part of the ramus, the articular might be somewhat different from that described for *Ichthyosaurus*, but this point must be settled by the study of better material.

Dentition.—In a recent note (Merriam, 1902) the writer stated that the dentition of *Shastasaurus* is differentiated. This information was based on the study of a small skull, supposed to belong to this genus. Later preparation of this specimen by the use of acids has made a more careful study of it possible, and it is found to differ so much from the typical Ichthyosaurs, and apparently also from *Shastasaurus*, that its reference to this group appears at present unwarranted.

A number of loose, conical teeth, with striated enamel crowns, have been collected in the limestones in which *Shastasaurus* remains occur, but as yet none have been found with recognizable specimens of that genus. Similar teeth occur in these beds in small jaws belonging to other groups, so that while some of them quite probably belong to *Shastasaurus* we cannot refer any of them to it with certainty.

Affinities and Classification

In the outlines of its structure, *Shastasaurus* shows itself clearly a member of the Ichthyopterygia. The skull, vertebræ, tail fin, extremities, and pectoral arch are of the type of those in *Ichthyosaurus*, and quite unlike the general aspect of the skeleton in any other group. In some of its characters, particularly the rib articulation in the dorsal region, the fusion of the hæmacentra to form chevron-bones, the form of the elements in the pelvic arch, and the specialization of the humerus in at least two species, it differs from the previously known genera of this order.

So far as approximation to a primitive type is concerned, the probable existence of a larger number of cervical intercentra than appear in other forms of this family is about the only really primitive character recognized. The separation of the radius and ulna, and the tibia and fibula, and the greater development of the pelvic arch are characters which, with the separate zygapophysial facets, indicate less complete accommodation of the Shastasaurian skeleton to purely aquatic conditions than we find in the Jurassic *Ichthyosaurus*. These characters are found also in the Triassic *Mixosaurus*, excepting those of the pelvic girdle, which has not yet been described from that genus; and to them should be added, as a common characteristic, the thickened spines of the upper arches. Others, notably the modification of the dorsal rib articulation, the formation of chevron-bones, and the shortening of the humerus, are specializations not found in this genus. The closest affinities of *Shastasaurus* are evidently with *Mixosaurus*, from which it is, however, sharply separated by the characters just mentioned, unless the structure of the forms in that genus be very different from that which has been ascribed to them.

The primitive characteristics found in the epipodial segments of the limbs and in the zygapophyses would probably be considered as sufficient to indicate somewhat greater age for this genus than the lower Jura with its longipinnate forms, in which a very small gap may exist between the epipodial bones. The specializations in the rib articulation, chevrons, and humerus, indicate a distinct line of descent which started with a form like *Mixosaurus*, and which in the upper Trias still retained some of its early characteristics, but had already gone a considerable distance along several lines of specialization that were never followed in the other genera. So far as we now know this line ended in the late Trias. Through the kindness of Professor W. C. Knight of the University of Wyoming, and Dr. Charles R. Eastman of Harvard University, the writer has been enabled to examine a series of vertebræ of *Baptanodon* from the Jurassic of Western North America, in order to determine whether possibly that genus is descended from *Shastasaurus*. The vertebræ are, however, of the *Ichthyosaurus* type, and *Baptanodon* can not be considered as derived from the typical Triassic forms of this region.

Should the classification of Baur (1887, p. 4) be accepted and the Ichthyopterygia be divided into three families, the Mixosauridæ, Ichthyosauridæ, and Baptanodontidæ, it will be necessary to add the representatives of the *Shastasaurus* group as a fourth division, for which the name Shastasauridæ is proposed. The distinguishing characters of this family will be founded in the peculiar articulation of the dorsal ribs, the form of the pelvic arch, and the presence of long-spined chevrons. If it is found advisable to bring all the genera of the Ichthyopterygia together in one family, *Shastasaurus* and its relatives should be grouped in a distinct sub-family, the Shastasaurinæ.

Distribution and Synonymy

That a group of marine reptiles with the characters of *Shastasaurus* would be confined within very narrow geographic limits is improbable, particularly as the occurrence of its remains points toward a fairly deep and open sea as its habitat. With a view to determining whether any of the Triassic Ichthyosaurian material described from other regions could possibly be considered as Shastasaurian, the writer has gone over such literature as is accessible to him, and the following list of species referred to the Triassic, outside of California and Nevada, has been compiled.

Mixosaurus atavus Quenstedt.
Mixosaurus cornalianus Bassani.
Mixosaurus nordenskjöldi Hulke.
Ichthyosaurus (?) *polaris* Hulke.
Ichthyosaurus (?) *rhœticus* Sauvage.
Ichthyosaurus (?) *carinatus* Sauvage.
Ichthyosaurus (?) *hectori* Lydekker.

Practically all of these species have been founded on very fragmentary material, in which a genus with characters like those of *Shastasaurus* might escape detection unless nearly perfect type specimens were available for comparison. Of the species mentioned, *hectori*, *polaris*, and *nordenskjöldi* do not appear to have yet been figured. The illustrations of *carinatus* and *rhœticus* are very imperfect. An outline drawing giving the limb structure of *cornalianus* was furnished by Baur, and Fraas has published good figures of scattered vertebræ of *atavus*, together with jaw fragments and a doubtful humerus.

The figure of *cornalianus* shows the structure of its anterior limb to be more primitive than that of either the anterior or the posterior limb of *Shastasaurus*, but gives us no hint as to the most important characters of that genus. The figures of the vertebræ of *atavus minor*, given by Fraas, show separate diapophyses and parapophyses low down on the centra, indicating that it is entirely different from *Shastasaurus*. The zygapophyses of the upper arches are also more nearly vertical and do not come so near to being in the same plane. It is clear that no very close relationship can be found with these two species or the genus which they represent.

In his description of *rhœticus*, Sauvage states that the diapophysis and parapophysis on one dorsal vertebra are united, and one might almost suppose that there existed here the modification found in the Californian species. However, in the description of another dorsal, he states that they touch in forming a figure eight, and in his illustration of this specimen, they are seen to be close together but quite distinct. The diapophysis appears also to be separate from the neurapophysial surface of the centrum so that the similarity to *Shastasaurus* is not so great as might appear from the description. On the other hand, notice should be taken of the very large di- and parapophyses, such as are not, to the writer's knowledge, found in *Ichthyosaurus*.

Concerning *carinatus*, little can be said excepting that both diapophyses and parapophyses are mentioned as being on a centrum which is evidently a dorsal.

Of the unfigured forms very little can be determined. According to the descriptions, Hulke's *polaris* agrees very well with the posterior dorsals of *Shastasaurus*, and later examination may show that it belongs to that genus.

It is hardly to be doubted that future exploration and investigation will bring to light remains of *Shastasaurus* at numerous points outside of the Pacific Coast region of North America.

Description of Species

Shastasaurus perrini n. sp.

Pls. 5, 6 and 7

The only specimen of this species known was discovered in the Cove some years ago by a collecting party working under the direction of Professor James Perrin Smith. Being too large to be handled without special appliances, it was left in the field till the fall of 1901, when Professor Smith generously turned it over to the University of California party then working in the Cove.

This specimen exhibits an unbroken series of eighty vertebræ, beginning near the anterior end of the dorsal region and ending well beyond the middle of the tail. The majority of the ribs from the lower side of the body and a number from the upper side lie next the vertebræ to which they were attached. The whole of the posterior arch and the most important parts of the hind limbs are present. Of the anterior girdle only a large fragment is left. The head and anterior limbs were in a portion of the slab which had been weathered or broken off. As yet no trace of them has been discovered.

This skeleton was found a considerable distance below the top of the layer of shaly limestone of the Trachyceras beds. As may be seen in Plate 5, fig. 1, the slab upon which it lies is largely made up of molluscan shells, among which *Halobia superba* is the most common form. A large specimen of *Tropites* rests against the lower side of the tail.

One of the most important characters of this species is found in the form of the vertebral centra, which are much longer than in the other known forms of the genus. In the second vertebra the ratio of length to height is 1:1.83, in the twenty-fifth 1:1.33, and in the fifty-fifth 1:54. The later caudals rapidly become shorter and higher. In the tenth vertebra of *osmonti*, which is near the place of the second of the *perrini* specimen, the ratio is 1:2.21. The variation in the relation of width to height of centra between the anterior and posterior ends of the column is much the same in *perrini* as in *osmonti*. The centra are deeply excavated on the anterior and posterior surfaces, which slope sharply from the margins to the centre. In those which could be examined the bony partition is not perforated, though it may be very thin.

The character of the rib articulation is not essentially different from the typical form described for the genus. The fifth to the fourteenth vertebræ present are covered by ribs and could not be examined. The fourteenth to the nineteenth are twisted away from the arches, and turned so that the inferior surfaces are uppermost. The ribs which covered these centra were removed and a cut made below the column to expose the dorsal surfaces. The rib articulations were successfully uncovered on the sixteenth to nineteenth and were found to be the same as those on the twenty-fifth (Pl. 5, fig. 2). The paraphophysis is gone, and the diaphophysis is connected with the superior articular surface. The lower side of the diapophysis, which swings forward to the anterior margin of the centrum, is somewhat narrower than in *osmonti*. On the twenty-seventh centrum the diapophysis is separated from the superior articular surface by a wide space. Unfortunately the twenty-sixth is turned over, and could not be examined without injury to the upper arch.

Opposite the pelvic girdle, or at about the fortieth vertebra, the diapophyses reach the lower side of the centra. They have here, however, nearly the same form as on the twenty-seventh. Back of the pelvic arch they rapidly become shorter, changing to an elliptical or circular outline. In this region they also move up the sides of the centra. On the sixtieth centrum they are about half way up the side. Beyond this point they could not be traced with certainty.

The upper arches do not vary greatly in height between the cervical and anterior caudal regions. Those of the anterior and middle dorsal region attain a slightly greater height than the others. In the cervicals and anterior dorsals the spines are relatively thicker than elsewhere, and the pedicels are much extended laterally. Back of the twenty-sixth vertebra, where the diapophyses separate from the upper articular surface, the bases of the pedicels show little, if any, lateral extension.

The lower arches begin at about the forty-fifth centrum. Possibly they were present anterior to this point, but no traces of them could be discovered. Articular surfaces for the chevrons are seen as far back as the sixty-fifth centrum. No indications of their existence are found beyond the bend in the tail.

The ribs in *perrini* do not have the peculiar modification of the head found in *altispinus* strongly marked. The articular surface shows a little of the outward and backward curvature seen in that species, but it is not so pronounced. In the dorsal region the whole proximal end of the rib is sharply twisted, so that its long diameter is moved almost eighty degrees from that of the middle of the shaft. In this twist the lower portion of the head and the flattened superior surface of the shaft are directed forward. The anterior side is deeply furrowed by a groove which begins on the upper side near the head, and may extend about two-thirds the length of the shaft. The posterior side is similarly channelled for about the same distance. The distal end of the shaft is always nearly circular in cross-section.

In the posterior portion of the dorsal region the ribs have broad heads, but the shafts are short and apparently without grooving.

Excepting the fragment probably representing the shoulder girdle, the limb and arch elements present have been described in detail in the general discussion of the genus.

The fragment resting upon the anterior dorsal ribs is too imperfect for satisfactory determination, but is probably the distal end of a coracoid. Its transverse diameter and thickness bear about the same relation to the dimensions of the anterior dorsal vertebræ as in *alexandræ*.

The following table of measurements gives the dimensions of the more important parts of this skeleton. All measurements are in millimeters. The letter *a* preceding a measurement indicates that it is approximated on a slightly broken specimen.

VERTEBRÆ

Number of vertebra in the series	Height of centrum	Width of centrum	Length of centrum	Height of upper arch	Width of upper arch	Thickness of spine near summit	Length of lower arch
2nd	22	*a* 24	12	....	....	....	....
3rd	....	....	*a* 13½	37	11.5	7.5	....
5th	....	....	*a* 14	39	....	....	....
9th	....	....	....	42	15	6.5	....
12th	....	....	....	45	18	6.5	....
15th	....	....	....	44	19.5	6.5	....
16th	....	....	20	....	....	....	....
17th	....	29	20	46	20	....	....
23rd	....	36	27	44	26	....	....
25th	37	....	27	45	27.5	9	....
27th	38	....	29	46	....	10	....
32nd	34.5	....	29	42	29	7	....
37th	*a* 38	....	29	44	*a* 28	7	....
46th	38	....	25	38	25	6.5	54
55th	37	....	24	30	*a* 19	5	....
62nd	34	....	15	....	....	....	....
78th	*a* 28	....	10	....	....	....	....

RIBS

	Width of head	Width of shaft 45 mm. from head
Rib opposite 6th vertebra	19	12.5
" " 22nd vertebra	17	9
" " 30th "	17	...
" " 37th "	25	8
" " 40th "	23	7
Length of apparently unbroken shaft of rib opposite 37th vertebra.		155

ARCHES

Coracoid (?)	
Greatest diameter of fragment	66
Thickness of unbroken end	18
Ilium	
Greatest length	44
Width of distal end	20
Thickness of distal end	9
Greatest diameter of proximal end	24
Ischium	
Greatest length	53
Greatest width	44
Width of proximal end	33
Thickness of proximal end	27
Thickness of distal end	9

Pubis	
Greatest length	48
Greatest width	52
Width of proximal end	26
Thickness of proximal end	12.5
Thickness of distal end	7

LIMB BONES

Femur	
Length	55
Width of proximal end	44
Width of middle of shaft	29
Width of distal end	52
Thickness through distal end at tibial articulation	22
Thickness through proximal end	24
Tibia	
Length	36
Width of proximal end	36.5
Width of middle shaft	27
Thickness of distal end	12(?)
Fibula	
Length	35
Width of proximal end	22
Width of middle of shaft	20
Width of distal end	32.5

Shastasaurus osmonti n. sp.

PLS. 8, 9, 10 AND 11

The type material of this species includes thirty-five vertebræ with the most important parts of the anterior arch and limbs. It was discovered by Mr. V. C. Osmont in the limestones near the Cove in June, 1901. About half of the bones, including the right limb, were embedded in several loose slabs lying at the foot of a limestone cliff, from which they had evidently but recently been separated, as other vertebræ and ribs were seen protruding from the rock close to them. The remains in the solid rock of the cliff were worked out in the fall of 1901 by Mr. H. W. Furlong, and were found to include part of a left limb of exactly the same dimensions as the right limb in the loose slab. The coracoids, and many of the cervical vertebræ, were found with the left limb. There can be no doubt that all of these remains belong to the one animal.

The vertebræ comprise individuals belonging to the cervical and dorsal regions. It is not certain that the series is complete, but judging from the gradual increase in size toward the posterior end, there are few, if any, gaps.

The most anterior individual is deeply biconcave and is, therefore, possibly neither atlas nor axis. On the other hand the large size of the intercentrum between it and the succeeding individual indicates that it was close to the anterior end of the column. It is not probable that it was further back than the third.

The following are the measurements of some of the best preserved centra and arches in the series. The position of the 7th, 11th, 17th, and 35th vertebræ could not be determined with absolute certainty, but is in each case not more than one or two vertebræ removed from the point in the column to which it is here referred. The height of the 1st and 3rd centra is given without and with (*h*) the inferior apophysis. Measurements in millimeters.

Centrum of series	Height	Width	Length	Height of diapophysis	Height of parapophysis
1st	40–48 *h*	43	21	20	10.5
3rd	40–46 *h*	48	22	23	10
7th	46	52	23	23	8
11th	49	53	27	29	4
17th	56	58	28	38	
25th	66	66	30	44	
35th	73	68	32	50	

Upper arch of cervical vertebra	
Height	60
Width half way between summit and posterior zygapophyses	17
Thickness half way between summit and posterior zygapophyses	15
Upper arch of anterior dorsal	
Height	66
Width half way between summit and posterior zygapophyses	25
Thickness half way between summit and posterior zygapophyses	13
Length of posterior zygapophysis	18.5
Width of anterior zygapophysis	10
Upper arch of middle dorsal	
Height	65
Width half way between summit and posterior zygapophyses	32
Thickness half way between summit and posterior zygapophyses	15
Length of posterior zygapophysis	18.5
Width of anterior zygapophysis	7

The dorsal ribs of this species show the characteristic backward twist of the rib-head and the flattening of the superior surface of the shaft (Pl. 9, fig. 6). The grooving of the shaft is stronger on the posterior side. The rib-head is slightly bent so that the posterior side is somewhat concave, also the upper part of the proximal surface turns outward. Both of these characters are much less pronounced than in *altispinus*.

The anterior arch (Pl. 10) is characterized by extreme thickness and relative narrowness of the coracoids (figs. 2 and 3). The scapula (figs. 4 and 5) is relatively heavier than that of *alexandræ*. The distal end of a clavicle present shows no distinguishing characters.

Following are the principal measurements compared with those of *alexandræ:*

	osmonti	*alexandræ*
Coracoid		
Length	160	170
Greatest width	*a*170	205
Width of proximal end	*a*110	144
Thickness of distal end	71	65
Greatest thickness of proximal end	60	62
Scapula		
Length	120	150
Greatest thickness of proximal end	52	52

a Approximate.

The anterior limbs of *osmonti* have been described in detail in the general discussion of the genus. As yet they are the only known bones representing the anterior limbs of this genus, except the fragment of a humerus with the specimen of *alexandræ*. The humerus of *osmonti* differs from that of *alexandræ* in being much thicker and in possessing a much narrower notch in the anterior border.

	osmonti	*alexandræ*
Humerus		
Greatest axial length	170	*a*190
Width of distal end	180	....
Greatest thickness proximal end	80	68
Thickness distal end	50	38
Width of anterior notch	10–20	40
Radius		
Length	95	....
Width	115	....
Thickness of proximal end	50	....
Ulna		
Length	71	....
Thickness of proximal end	30	....
Radiale		
Width	95	....
Thickness of proximal end	30	....

a Approximate.

Shastasaurus alexandræ n. sp.

PLS. 12 AND 13

This species is represented by a specimen collected a quarter of a mile south of the Cove by the party under Mr. H. W. Furlong. It was found a short distance below the contact between the Atractites beds and the Trachyceras beds. The specimen includes the greater part of a skull, nearly all of the pectoral girdle, part of a humerus, fifteen or sixteen vertebræ belonging to the anterior portion of the column, and numerous ribs.

The cranium has already been described in detail as the only one certainly known to belong to a member of this genus. It is essentially like that of *Ichthyosaurus*. The portion of a humerus which is present shows that element to have been much thinner at both extremities than in *osmonti*. The anterior notch is also very different, being much wider and relatively shallower.

The coracoids like the humerus are thinner at both extremities than in *osmonti* and are much wider distally. The anterior distal hook is in consequence of this somewhat longer and the anterior notch deeper. The clavicle is long and slender. The interclavicle is unknown.

The anterior portion of the vertebral column runs up to the foramen magnum and is probably complete. Immediately behind the back of the skull, and in close proximity to it, are two small indeterminate ossicles in the position which the separate pieces of the upper arch of the atlas would naturally occupy. Following them is a vertebra-like body, which does not seem to be biconcave. Its dimensions are nearly the same as those of a deeply amphicœlous centrum immediately behind it, and it is possibly the atlas. The first certainly determinable vertebra is the second large element behind the parietals. It is deeply biconcave, the excavated end surfaces sloping gradually to the center. On one side of this centrum there is an oblique truncation at each end. Against one of these there rests a small piece of bone which is probably an intercentrum. The second centrum behind this one, the fourth, is well exposed, showing the sides and anterior end. The lower side of the anterior end is produced downward as an apophysis, against the anterior face of which an intercentrum has rested. The inferior apophysis gives to the front face of this centrum a height as great as the breadth and makes the cross-section pentagonal. On this centrum, as on the three following it, the diapophyses are high and broad. They narrow toward the top and are connected with the upper articular surfaces. The parapophyses are relatively small, their height being considerably less than half that of the diapophyses. On the eighth the parapophysis is abnormally large and is also entirely out of its natural position, being on the posterior margin. On the ninth it is in its normal position and very small.

The upper arches, which are well shown on the fifth and seventh, are high and rather slender. The spines are very thick, being almost circular in cross-section. The zygapophyses are large and strong. The bases of the pedicels project laterally over the diapophysial ridges.

Two or three of the ribs which are present show both the capitulum and tuberculum. The former is, however, in all cases very small. On several other well preserved ribs there is only a broad tuberculum, such as is seen in thoracic ribs of the other species.

Measurements:

4th vertebra	
Height of centrum including inferior process	49 mm.
Width of centrum	49
Length of centrum	22
Height of diapophysis	22
Height of parapophysis	9
6th vertebra	
Height of centrum, approximately	44
Length of centrum	27
Height of upper arch	74
Width of upper arch half way between summit and posterior zygapophyses	18
Thickness of upper arch at summit	18
Height of diapophysis	24
Height of parapophysis	9
8th vertebra—Length of centrum	28
9th vertebra—Length of centrum	30

Shastasaurus careyi n. sp.

Pl. 16, Figs. 3 and 4

Among the most interesting remains that have been obtained from the Shasta County Triassic are several gigantic vertebræ and portions of ribs belonging with them. The first determinable specimens were found by Mr. E. R. Carey in the small exposure of limestone on Bear Mountain, twenty miles northeast of Redding. Other less perfect examples were obtained by Mr. V. C. Osmont, Mr. H. W. Furlong, and the writer at the Cove, near Madison's ranch.

The vertebræ collected by Mr. Carey are considerably wider than high (180 mm. to 160 mm.), and the short, broad diapophyses do not reach below the middle of the centrum. The parapophyses are very rudimentary, being represented only by small, rounded tubercles near the anterior margin of the centrum. The length of the centrum (60 mm.) is relatively less than in any of the other species. A rib-head resting against the side of one of the centra shows no trace of a capitulum. Part of a thick upper arch which is present shows strong zygapophyses.

The width of the centra and the shortness of the diapophyses of these vertebræ seem to indicate that they belong in the cervical or anterior dorsal region. The height of the rib-head shows that the diapophysis is not abnormally shortened owing to extensive articulation of the tuberculum against the upper arch. The very rudimentary parapophyses would, taken by themselves, point to a more posterior position in the column than is suggested by the other characters. The form of the cross-section and length of the diapophysis are, however, more nearly constant characters than the relative size of the disappearing parapophysis, and it seems to the writer that in this form the reduction of the parapophyses has possibly gone farther in the cervical region than in the other known species.

The dimensions of these vertebræ and ribs show that the individuals to which they belonged ranked among the largest known Ichthyopterygia. If the centrum just described be supposed to belong as far back in the column as the tenth in *osmonti*, and if the ratio of its size to that of the thirty-fifth were the same as in that species, the thirty-fifth would have a diameter of 245 mm.

Although the quantity of material at hand is insufficient for satisfactory diagnosis of this form, it would seem that the shortness of the centra, the possible unusual reduction of the parapophyses, and the large size, indicate a distinct species. It is, of course, possible that all of these characters could belong to old individuals of some of the other forms described. It appears very doubtful to the writer, however, whether the centra would become relatively shorter with age; while greater reduction of the parapophyses would almost be expected in one of the larger species of the genus.

The following are the measurements of the type specimens of *careyi*:

Width of rib-head 55 mm. from proximal end	55 mm.
Estimated width of rib-head at proximal end	75
Width of second centrum	180
Height estimated certainly within 5 mm. of actual size	160
Length of centrum	60

Shastasaurus altispinus n. sp.

Pl. 14, Fig. 5, and Pl. 15

The specimens representing this species were found embedded in two loose slabs lying close together at the foot of a steep bluff near the Cove, three miles from Madison's ranch, on Squaw Creek. The horizon at which they occurred seemed to be near the base of the Atractites beds. The bones all appear to belong to one individual. They include five vertebræ from the posterior and middle dorsal regions, several well preserved ribs, one complete limb bone, a fragment of another, and a piece of a large arch bone.

On four of the vertebræ the summits of the diapophyses are below and disconnected from the upper surface of the centrum, while the lower ends are relatively near the inferior surface (Pl. 15, fig. 1). The diapophysial ridges on these individuals are long, slender, and much constricted at the point where the lower part swings forward. As is shown in the table of measurements following, the height of the centrum is slightly greater than the width. The greatest breadth is considerably below the middle, which gives the centrum a pear-shaped cross-section.

Measurements of a centrum on which the diapophyses do not reach the summit.

Height	97 mm.
Greatest width	92
Length	46
Height of diapophysial ridge	62
Width of diapophysis at constriction	9
Greatest width of lower extremity of diapophysis	21
Height of upper arches with these centra	120
Antero-posterior diameter of spines at widest point above posterior zygapophyses	34–32
Transverse diameter at the point where antero-posterior was taken	27–27

The other vertebra (fig. 2) has a length of 41 mm. and is consequently somewhat smaller than the four already discussed. Its diapophysial ridge reaches the summit of the centrum, and the articular surface is confluent with that for the reception of the upper arch. This centrum belongs apparently to a middle dorsal and the other four followed close behind, probably separated from it by only a few individuals.

One of the distinguishing characters of this species is found in the form of the upper arches, which are remarkably high and thick (figs. 3 and 4). The margins of the spines are very thin, particularly on the lower portion of the anterior side. Excepting these blade-like edges, the cross-section of the shaft of the spine is almost circular near the summit. The height of the spine is relatively greater than in the other forms. As indicated in the table of measurements, this dimension is relatively greater than in vertebræ from a portion of the column of *osmonti* slightly anterior to that from which these came, and also greater than that of the late dorsals of *pacificus*. The zygapophyses are not well preserved, but enough is present to show that they are rather slender and that the right and left facets are not united. The pedicels of the arches show no lateral projection. The general form of the arches present is somewhat similar to that of the cervicals of *alexandræ*. They are, however, too large for cervicals at all comparable to those of other species as regards the relation of their dimensions to those of the middle dorsals. The pedicels are also narrower than in the cervicals. Should it ever appear that cervical arches are here mingled with dorsal vertebræ, this species would be even more sharply separated from the others than it is now held to be.

The *ribs* (figs. 5 and 6) associated with the vertebræ just described were most of them lying in such a position as to permit of little doubt as to their having been practically undisturbed. On the broad heads a marked constriction of the middle portion of the articular surface is produced by profound excavation of the posterior side. The upper portion of this surface is considerably smaller than the lower and its long axis inclines backward and away from it. The surface also bends sharply outward, deviating as much as thirty-five degrees from the plane of the lower face. The shaft of the rib is almost triangular in cross-section. The upper surface is slightly convex, while the anterior and posterior sides are grooved.

Such ribs as those that have just been described are ordinarily associated with vertebræ in which at least the superior portion of the articular surface rests against the upper arch. There seems to be no question that there is represented here a peculiar mode of attachment, in which the loss of the lower rib head is compensated for in the manner described above (page 76).

Measurements of a Rib

Length of portion of proximal surface of head below constriction	31 mm.
Breadth of lower surface	20
Length of portion above constriction	32
Breadth of portion above constriction	14
Height of shaft 90 mm. from proximal end	24
Width of flattened superior surface	19

The two *limb bones* are like the notched elements on the anterior borders of the limbs of the longipinnate Ichthyosauria. Excepting on the notched side, their margins show a regularly rounded outline and it is, therefore, not probable that they represent either the radius or the tibia, but were situated in the metapodial or phalangial segments. The perfect specimen is represented by fig. 5, Pl. 14. The following are their dimensions:

	Perfect specimen	Fragmentary specimen
Greatest transverse diameter	85 mm.	..
Greatest axial diameter	67	74 mm.
Greatest thickness	35	37
Depth of notch	20	25

Shastasaurus pacificus Merriam

Pl. 14, Figs. 1 and 2

Shastasaurus pacificus Merriam. Am. Jour. Sci. Vol. 4, 1895, p. 56.

The type species of the genus *Shastasaurus* was based on a series of eight vertebræ with several fragments of ribs and two arch bones, one of which was very fragmentary, the other being practically perfect. The vertebræ were recognized as pre-caudals, and, being associated with what were supposed to be certainly coracoids, they were described as doubtful anterior dorsals. A re-examination of the type shows the vertebræ to have been without chevrons, while the diapophyses occupy the same position as those near the pelvic arch, so that they may be considered as posterior dorsals.

The elements which were taken to be coracoids (Pl. 14, fig. 2) are very different from both the coracoid and the scapula of the two species in which these bones are known. This difference appears in the general outlines, and more particularly in the form of the proximal end (text fig. 1), which is very characteristic on both coracoid and scapula. The whole form is most closely approximated, although not exactly duplicated, in the pubis of *perrini*, and inasmuch as the vertebræ with which they were associated are quite distant from the region of the shoulder girdle, they probably correspond to that element.

The only other specimen showing vertebræ from this portion of the dorsal region is the skeleton of *perrini*. From this it differs very considerably in length of centrum and thickness of neural spine.

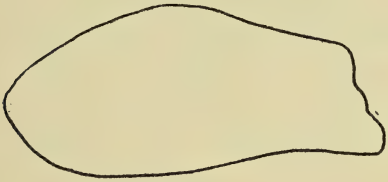

Fig. 1

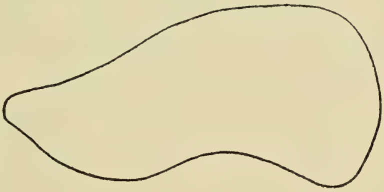

Fig. 2

Fig. 1. Cross-section of proximal end of left (?) pubis. *S. pacificus.*
Fig. 2. Cross-section of proximal end of right coracoid. *S. alexandræ.*

The centra are much shorter than in *perrini*, and somewhat longer than in all of the other known species. At the present time we cannot determine definitely the relations of *pacificus* to the better known species, and it is not impossible that when other parts of the skeleton of those forms are known it will be found that some one of them should be included in *pacificus*.

Measurements:

Vertebræ	
Height of first centrum in cross-section*	68 mm.
Width	70
Length of fourth centrum	36
Height of second upper arch	67
Width " " "	35
Thickness of spine of sixth upper arch	14
Pubis	
Greatest length	130
Width of proximal end	95
Thickness	46

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* The original measurement of height was made on an imperfectly exposed vertebra and measured only to the neural groove.

FORMS FROM MIDDLE TRIASSIC OF NEVADA, CYMBOSPONDYLUS GROUP

Cymbospondylus Leidy

Proc. Philad. Acad. Sci., 1868, v. 20, p. 177.

This genus was founded by Leidy upon several fragmentary and imperfectly prepared vertebræ "from the Triassic rocks of Star Cañon, Humboldt Co. (Nevada), and from the Toiyabe Range, northeast of Austin, Nevada." With the type specimen from New Pass, in the Toiyabe Range, are "two shells which appear to be *Ammonites blakei* Gabb and *Posidonomya stella* Gabb."

According to Professor James Perrin Smith the presence of *Am. blakei* indicates that these beds are middle Triassic and consequently older than those from which the saurians were obtained in Northern California. These remains, therefore, represent the oldest known Ichthyopterygians of this coast, and among the oldest that have ever been discovered. Two species were described by Leidy, *C. piscosus* and *petrinus*. *C. piscosus* is the first mentioned and must be taken as the type of the genus. Following are the principal parts of Leidy's description of the type specimen, which consists of portions of five vertebræ.

Cymbospondylus piscosus Leidy

Pl. 16, Figs. 1 and 2

"The body of the vertebræ is deeply biconcave, as in *Ichthyosaurus*. The length is considerably less than the breadth. The under side is plane fore and aft, but the margins are slightly prominent and bevelled. The sides are slightly concave and provided with a short and robust process for the head of a rib. The neural arch with its spine visible in one vertebra along the broken margin of the specimen, rises above the body about one and one-half times its depth, and its abutment exhibits the remains of another articular process for the rib. The neural canal is triangular."

From New Pass, in the Toiyabe Range, northeast of Austin, Nevada.

From this diagnosis the writer found it impossible to determine the affinities of *Cymbospondylus*, and through the kindness of Dr. Charles R. Eastman, the type specimens of Leidy's species of Nevada Triassic saurians were obtained for study from the Whitney collection at Harvard University. The type of *C. piscosus* was not sufficiently well prepared to show the characters of the vertebræ, which Leidy apparently did not understand. The matrix was, therefore, removed from the sides of the centra and arches. The form of the vertebræ shows them to belong to the anterior dorsal region. The centra are a little longer than in most Ichthyosauria and are deeply amphicœlous, the concave surfaces beginning close to the periphery and sloping sharply the whole way to the centre. There is but one surface of articulation for the rib-head. This is situated on a long, broad, and prominent ridge, which begins on the upper side of the centrum and runs downward and forward to the anterior margin. At the superior end it is very broad. It narrows in the middle and widens again at the lower end. The upper portion of the articular surface seems to be continuous with that upon which the upper arch rests. The broad lower end runs to the anterior margin of the centrum. The pedicels of the upper arches are seen to be considerably extended laterally toward the ribs. The spines are moderately high and quite thick, but show no trace of a lateral rib. The zygapophyses are large and strong. They are not brought into the same plane on the right and left sides and are evidently paired. They come nearer to being perpendicular to the long axis of the spine than in *Shastasaurus* and the arches are more nearly erect.

The lateral ridge of the centrum corresponds to the diapophysis. No trace of a parapophysis is present. The diapophysial ridge is divided into a rough upper face and a smoother lower surface by a salient portion situated at the point where the lower end bends forward. The rib articulation was solely upon the diapophysis and principally with the smoother lower surface.

Measurements of vertebræ of *C. piscosus*:

Height of centrum, 4th vertebra	36 mm.
Width " " "	38
Length " " "	23
Height of upper arch, 2nd vertebra	49
Width of spine " "	23
Thickness of spine " "	$8\frac{1}{3}$

Cymbospondylus petrinus Leidy

Pl. 16, Figs. 4 and 5

The second species, consisting of the greater part of three centra with portions of two arches, is described by Leidy as follows:

"They apparently indicate a much larger species of the same genus as the former, the vertebral body having the same form. The sides of the articular funnels are convex outwardly from the centre, which deepen more rapidly at the inner third of the surface. One specimen retains the neural arch without its spine, and a short, robust, costal process, extending from near the bottom of the arch almost half the depth of the body. A second vertebra is singularly distorted, apparently as if the bone had been in a plastic condition."

From Humboldt, Nevada.

After uncovering the costal processes of the vertebræ of this species they were seen to be essentially the same as those of *C. piscosus*. The centra are, however, much shorter than in the type species, the ratio of length to height being 1:2.35. The form of the anterior and posterior surfaces of the centra is also very different. Instead of sloping sharply from margin to centre, the concave surfaces slope gently from the periphery for about two-thirds of the distance to the centre and then drop down very rapidly to the middle, making a central depression which almost meets a similar one on the opposite side.

The vertebræ present are evidently middle dorsals of a species much larger than *piscosus*.

The measurements of a somewhat distorted centrum are as follows:

Height of centrum	87 mm.
Width "	87
Length "	37

Cymbospondylus (?) grandis Leidy

PL. 16, FIG. 3

Chonespondylus grandis Leidy. Proc. Phila. Acad. Sc., Vol. 20, 1868, p. 178.

A third species, based on a fragment of a caudal from Star Cañon, Humboldt Co., was made the type of a new genus, *Chonespondylus*, by Leidy. There is, however, nothing to indicate that it represents a group distinct from *Cymbospondylus*. So far as can be determined from the fragmentary type specimen, this species has combined in it the length of vertebra found in *C. piscosus* and the peculiar flaring articular funnels of *C. petrinus*. The animal from which this vertebra came was very much larger than that indicated by the types of *piscosus* and *petrinus*.

MEASUREMENTS OF TYPE SPECIMEN

Estimated height of centrum	120 mm.
Estimated width of centrum	84
Length of centrum	58

AFFINITIES OF CYMBOSPONDYLUS

So far as can be determined with the material at hand, *Cymbospondylus* is closely related to *Shastasaurus*, having the peculiar form of rib articulation which has been described for that genus, and it is possible that it will be shown later that the two are identical. The species which we now have, differ from *Shastasaurus* in possessing much broader and heavier diapophyses, the lower ends of which are continuous with the anterior margin. In the well preserved upper arches of *C. piscosus* the spines are relatively thin, there is no trace of a lateral rib, the zygapophyses stand more nearly at a right angle to the axis of the spine than in *Shastasaurus* and the whole arch comes nearer to an erect position than in the anterior dorsal region of that genus. With the material available, it is advisable to keep the older *Cymbospondylus* type distinct from the *Shastasaurus* group of the Upper Triassic. Later discoveries may show that they cannot be separated generically, or may bring out differences much more important than those indicated in the specimens now known.

POSTSCRIPT

After the description of *Cymbospondylus* was partly printed, a good collection of saurian material was obtained from the middle Triassic of Nevada. The bones are all embedded in blocks of very hard limestone, from which it will require many months of careful work to free them. At the present time little more can be determined than that several specimens, which appear to belong to *C. petrinus*, show a number of peculiar characters not heretofore noticed in any of the forms which have been examined. The results of a study of this material will appear in a later paper.

BIBLIOGRAPHY

Bassani, F.

1886—Sui fossili e sull' età degli schisti bituminosi Triasici di Besano. Atti della soc. Ital. di sc. natur., vol. xxix, p. 20.

Baur G.

1887—Ueber den Ursprung der Extremitäten der Ichthyopterygia. Bericht der xx. Versammlung des Oberrhein. geol. Ver., vol. xx, 1887. (2) Amer. Naturl., vol. xxi, p. 840.

Dames, W.

1895—Die Ichthyopterygier der Triasformation. Sitzb. der. Acad. der Wiss. Berlin, 1895, p. 1045.

Fraas, E.

1891—Die Ichthyosaurier der Süddeutschen Trias- and Jura-Ablagerungen. Tübingen, 1891.

1896—Schwäbische Trias-Saurier. Stuttgart, 1896.

Hector.

1874—Trans. New Zealand Inst., vol. vi. p. 355.

Hulke.

1873—On some Vertebrate Remains from Spitzbergen. Bihang K. svenska Vet. Ak. Handlingar., vol. i, no. 9.

Leidy, J.

1868—Notice of some Reptilian Remains from Nevada. Proc. Philad. Acad. Sc., vol. xx, p. 177.

Merriam, J. C.

1895—On some Reptilian Remains from the Triassic of Northern California. Am. Jour. Sc., vol. L, p. 55.

1902—Triassic Reptilia from Northern California. Science N. S., vol. xv, p. 411.

Meyer, H. von.

1855—Zur Fauna der Vorwelt.

Quenstedt.

1852—Handbuch der Petrefactenkunde, p. 129, pl. vi, figs. 7–10.

Sauvage, H. E.

1876—Note on the remains of Ichthyosauria from the Rhætic of Saône and Loire. Ann. Sc., vol. vii–viii, art. 6.

1883—Recherches sur les Reptiles Trouvés dans l'Etage Rhétien des Environs d'Autun. Ann. Sc., vol. xiv, art. 3.

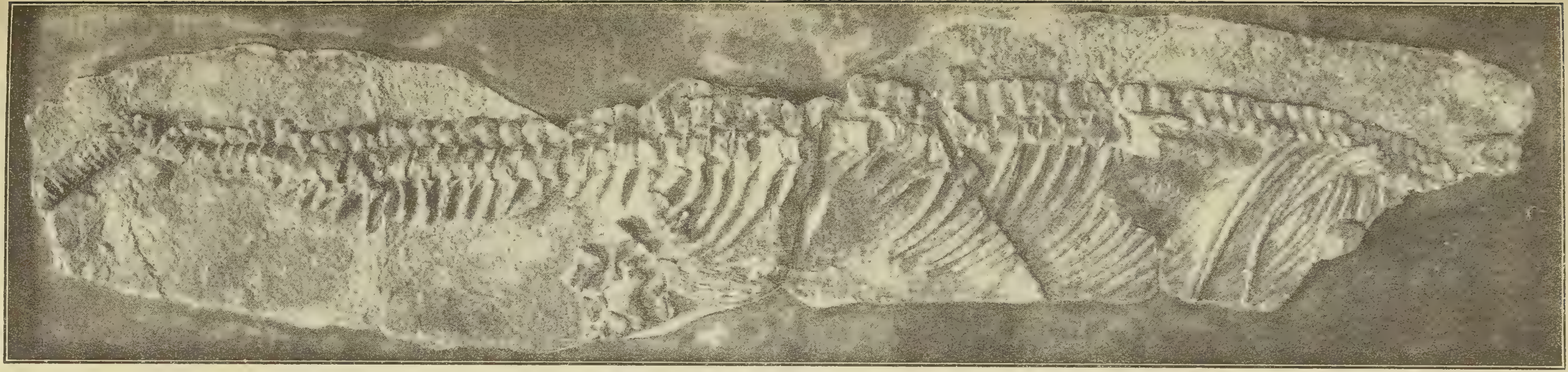

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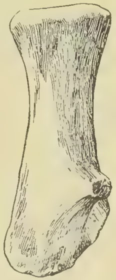
FIG. 1. Skeleton in relief on the original slab. About one-tenth natural size.

FIG. 2. Right ilium, posterior side. Three-fourths natural size.
FIG. 3. Right ilium, lateral view. Three-fourths natural size.
FIG. 4. Right ischium. Three-fourths natural size.
FIG. 5. Right pubis. Three-fourths natural size.



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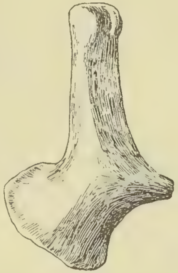

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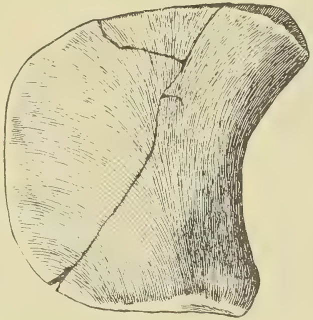

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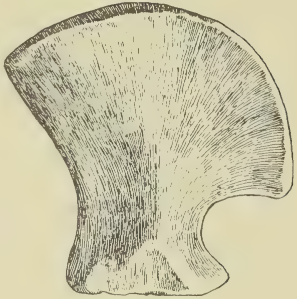

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Shastasaurus perrini n. sp.

All figures are from the type specimen

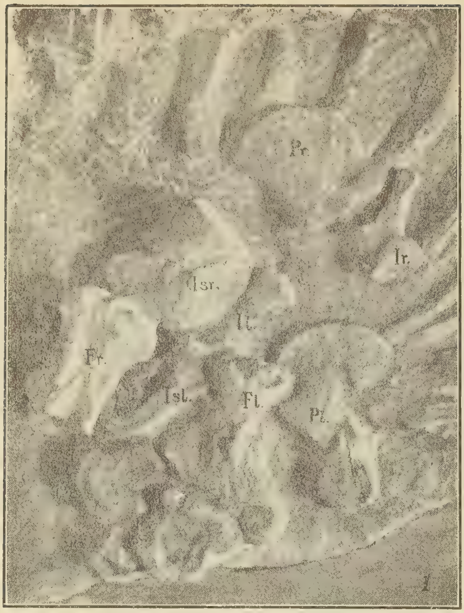


FIG. 1. Posterior arch and limbs, showing position of elements in the matrix. Ir, right ilium; Il, left ilium; Isr, right ischium; Isl, left ischium; Pr, right pubis; Pl, left pubis; Fr, right femur; Fl, left femur. One-third natural size.

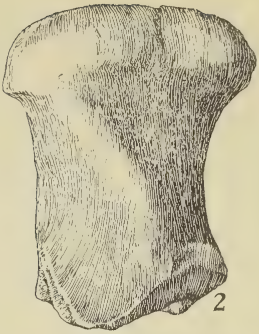


FIG. 2. Right femur, side view. Three-fourths natural size.

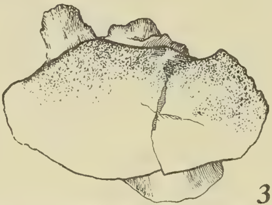


FIG. 3. Right femur, proximal end, showing the position of its longer transverse diameter with reference to that of the somewhat damaged distal end. Three-fourths natural size.

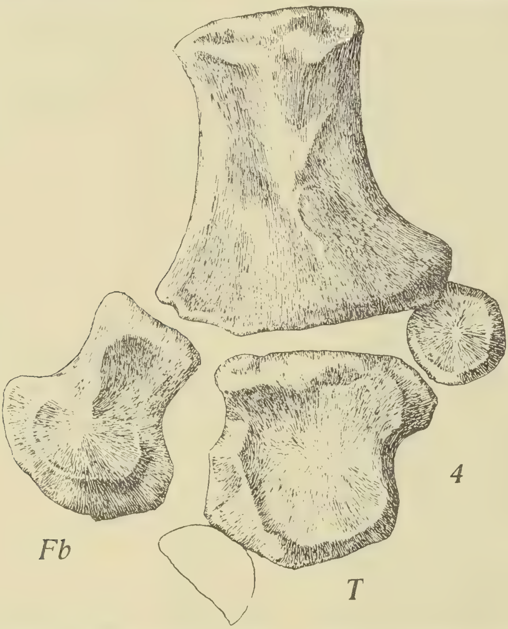
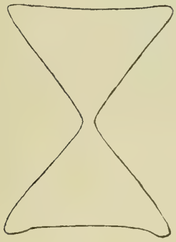


FIG. 4. Left posterior limb. Fb, fibula; T, tibia. The small ossicle between the tibia and femur is probably a loose phalanx like two near the proximal end of Pl in figure one. The fragment of an ossicle shown in outline between the tibia and fibula possibly represents the intermedium. Three-fourths natural size.

Shastasaurus perrini n. sp.

All figures are from the type specimen



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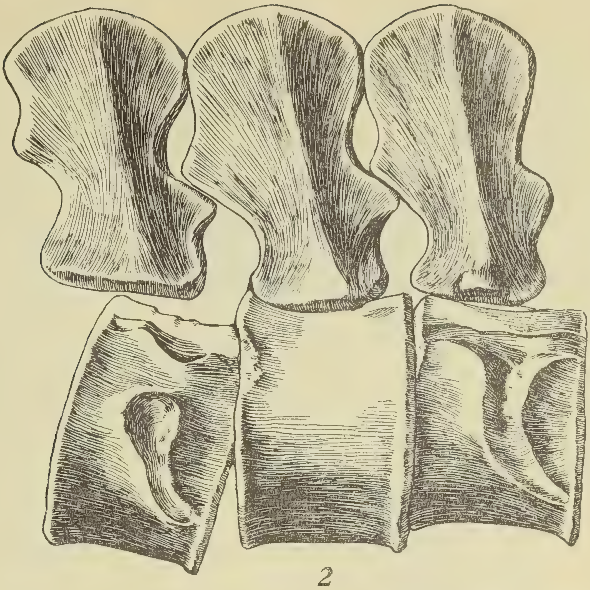

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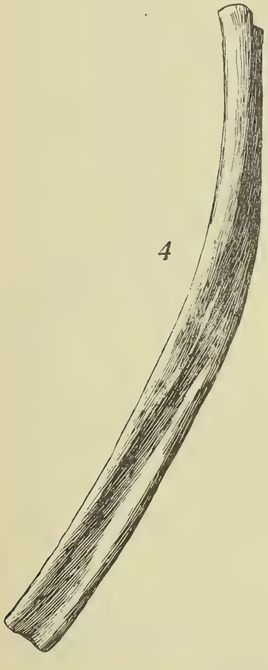
FIG. 1. Antero-posterior section of posterior dorsal vertebra. Constructed from the 32nd and 33rd vertebræ of this series.

FIG. 2. Dorsal vertebræ; 25th to 27th of this series.



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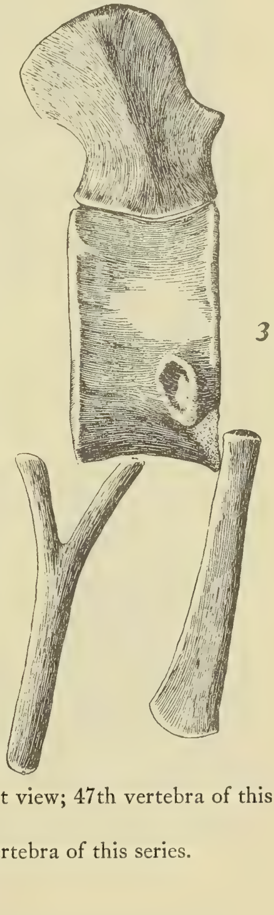

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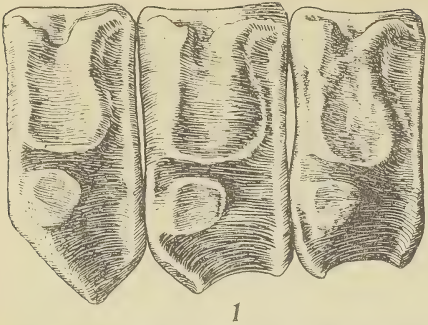
FIG. 3. Caudal vertebra, with lower arches in side and front view; 47th vertebra of this series.

FIG. 4. Anterior side of a left dorsal rib. Opposite 22nd vertebra of this series.

Shastasaurus perrini n. sp.

All figures are from the type specimen, and are represented three-fourths natural size



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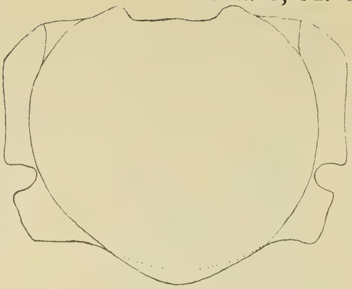

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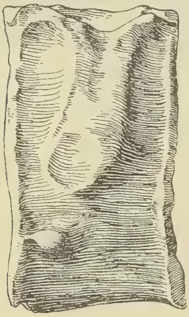
FIG. 1. Cervical centra showing well developed di- and parapophyses and facets for reception of intercentra. First three vertebræ in this series.

FIG. 2. Cross-section of 3rd cervical centrum of this series. The position of the base of this centrum behind the inferior apophysis is shown by a dotted line.



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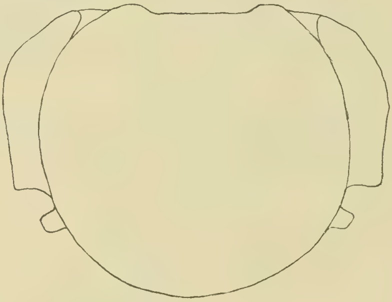

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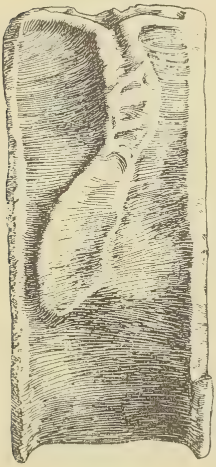
FIG. 3. Anterior dorsal centrum showing greatly reduced parapophysis; 11th vertebra of this series.

FIG. 4. Cross-section of 11th vertebra of this series.



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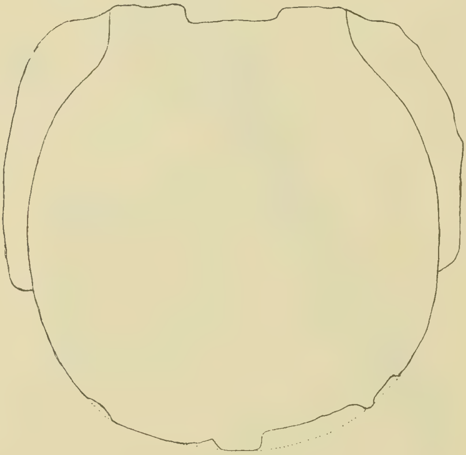

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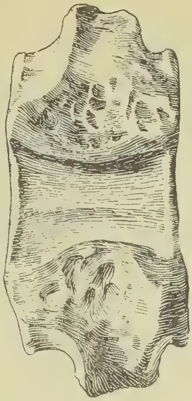
FIG. 5. Posterior or middle dorsal centrum, 35th of this series.

FIG. 6. Cross-section of 35th centrum of this series.

Shastasaurus osmonti n. sp.

All figures are from the type specimen, and are represented three-fourths natural size



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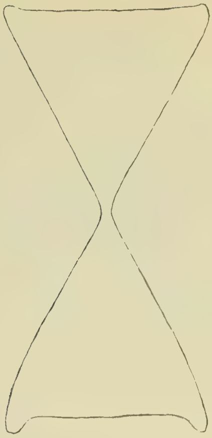

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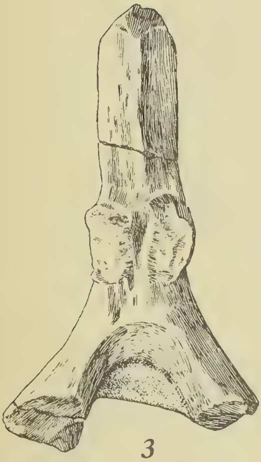
FIG. 1. Superior side of 11th centrum of this series.

FIG. 2. Antero-posterior section of 35th centrum of this series.



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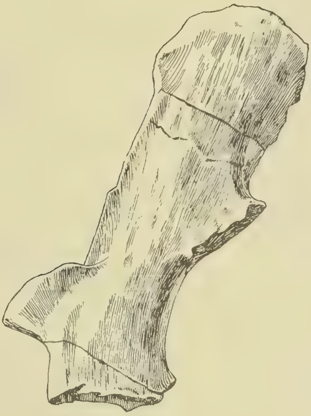

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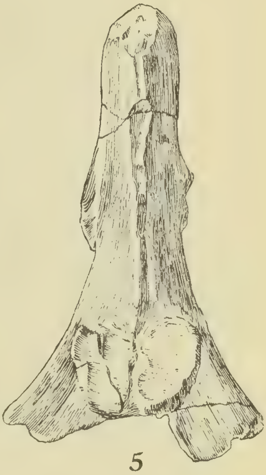

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FIG. 3. Posterior view of an anterior dorsal arch, showing separate zygapophysial facets. The summit of the spine should probably be represented as slightly excavated, but could not be sufficiently well prepared to show this character.

FIG. 4. Side view of anterior dorsal arch shown in figure 3.

FIG. 5. Anterior view of anterior dorsal arch shown in figure 3.

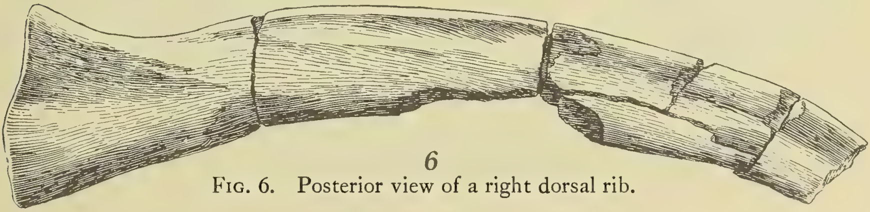

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FIG. 6. Posterior view of a right dorsal rib.

Shastasaurus osmonti n. sp.

All figures are from the type specimen, and are represented three-fourths natural size

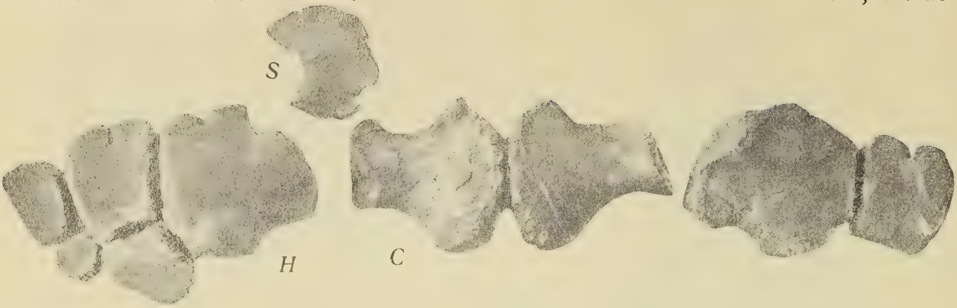

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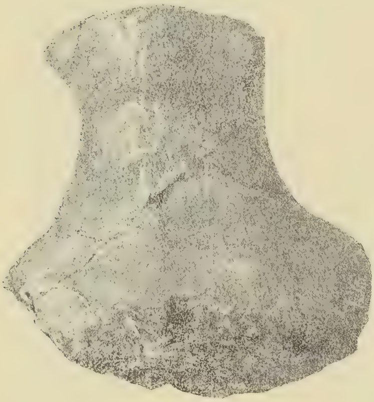
Fig. 1. Lower side of anterior arch and limbs. S, right scapula; C, right coracoid; H, right humerus. A little less than one-eighth natural size.



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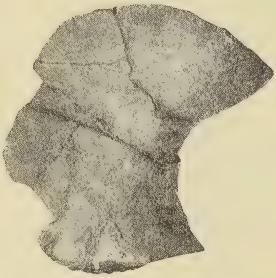

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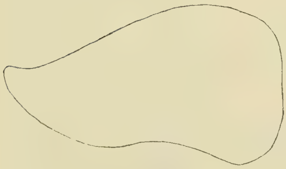
Fig. 2. Upper side of right coracoid. A little more than one-fourth natural size.
Fig. 4. Upper side of right scapula, about three-tenths natural size.



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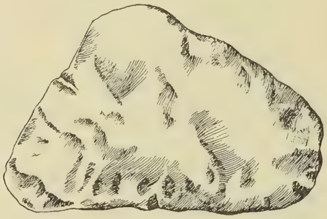

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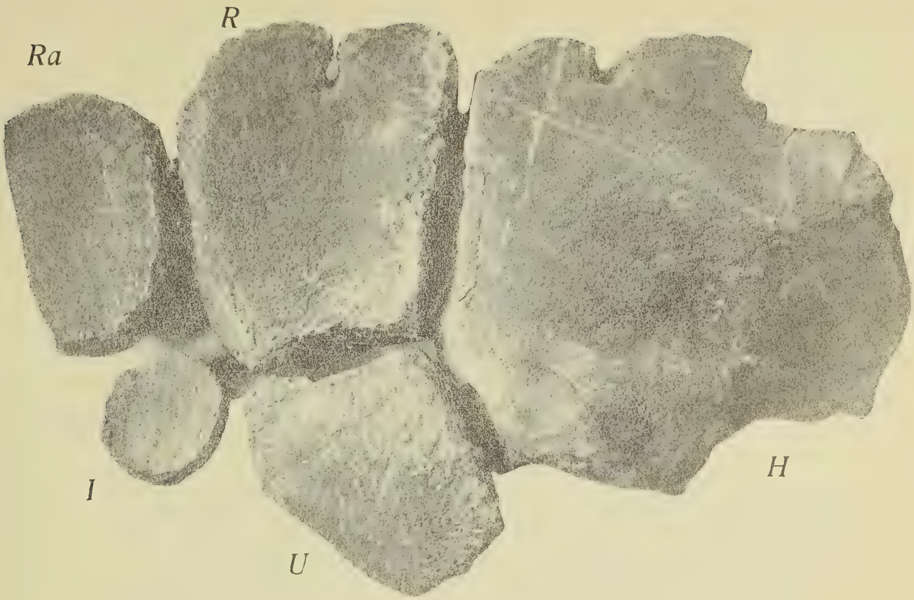
Fig. 3. Cross-section of proximal end of right coracoid, one-third natural size.
Fig. 5. Proximal end of right scapula, one-half natural size.

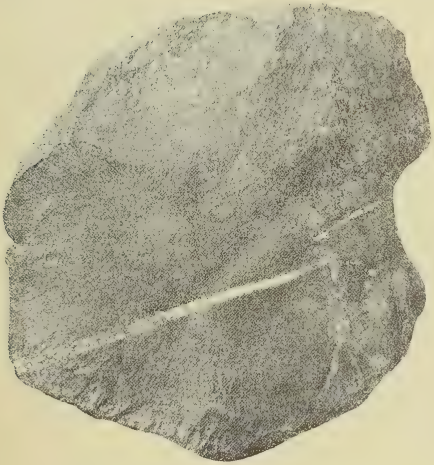
Shastasaurus osmonti n. sp.

All figures are from the type specimen



1

FIG. 1. Lower side of right limb. H, humerus; R, radius; U, Ulna; Ra, radiale; I, intermedium. A little more than one-third natural size (.36).



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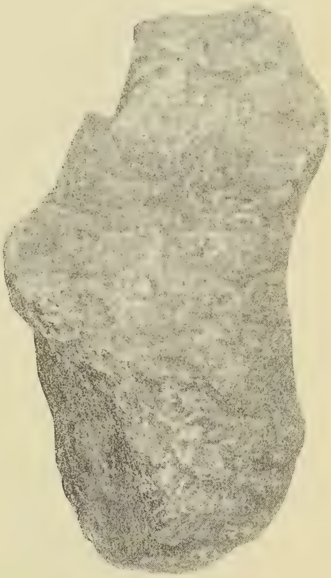

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FIG. 2. Upper side of left humerus. One-third natural size.
FIG. 3. Proximal end of left humerus. One-half natural size.

Shastasaurus osmonti n. sp.

All figures are from the type specimen

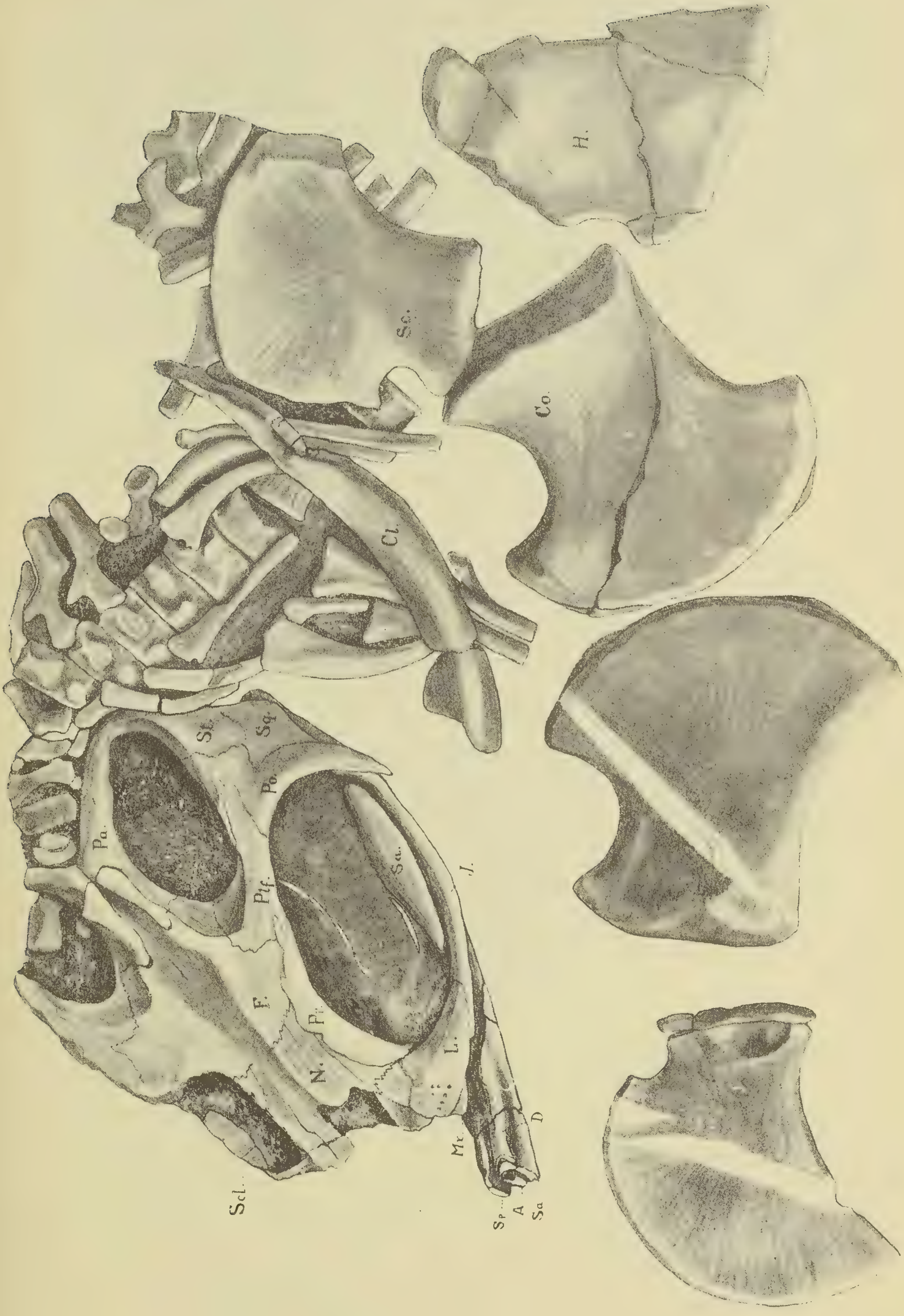
EXPLANATION OF PLATE 12

Shastasaurus alexandræ n. sp.

The type specimen, represented two-ninths natural size

Excepting the right scapula and the left humerus, the bones have not been moved from the positions which they occupied in the matrix. The right scapula was doubled underneath the coracoid and the humerus fragment partly covered the left coracoid. The right scapula and coracoid were cut by a somewhat irregular vein of calcite.

Co, left coracoid
Sc, left scapula
Cl, left clavicle
H, left humerus
D, dentary
A, angular
Sa, supra-angular
Sp, splenial
Mx, maxillary
L, lachrymal
J, jugal
N, nasal
F, frontal
Pr, prefrontal
Ptf, postfrontal
Pa, parietal
St, supratemporal
Sq, squamosal
Po, postorbital
Scl, sclerotic plates


H.
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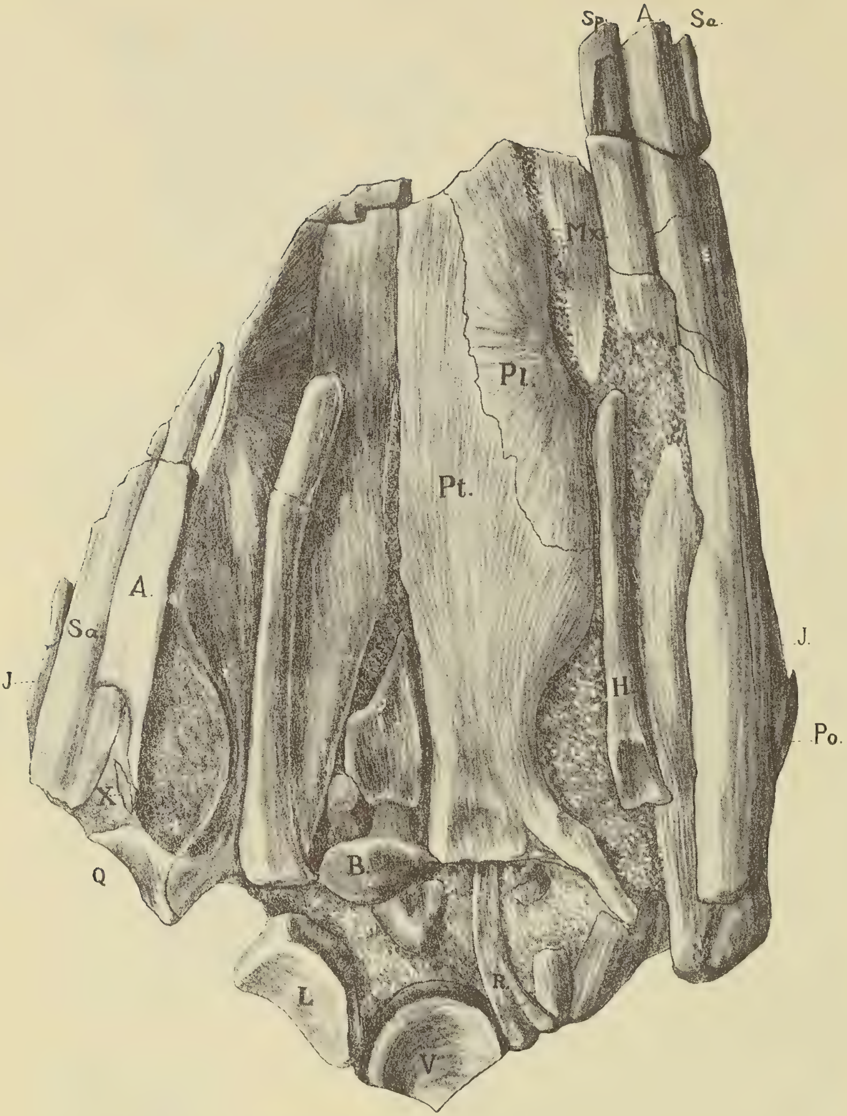

Shastsaurus alexandræa n. sp.

Lower side of the skull of type specimen, represented one-third natural size

V, cervical vertebra, probably the third
R, cervical rib. The head slightly injured in preparation
H, thyrohyal
A, angular
Sa, supra-angular
Sp, splenial
X, coronoid (?)

Mx, maxillary
Pl, palatine
Pt, pterygoid
Q, quadrate
J, jugal
Po, postorbital
B, basioccipital
L, undetermined element

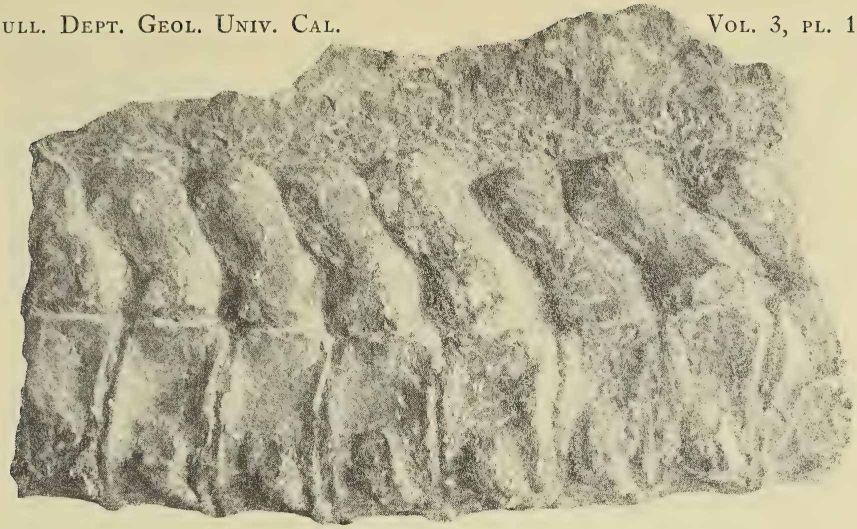
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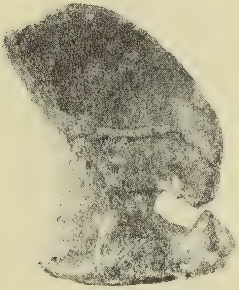
Fig. 1. **Shastasaurus pacificus**, Merriam. Posterior dorsal vertebræ of type specimen represented about four-tenths natural size.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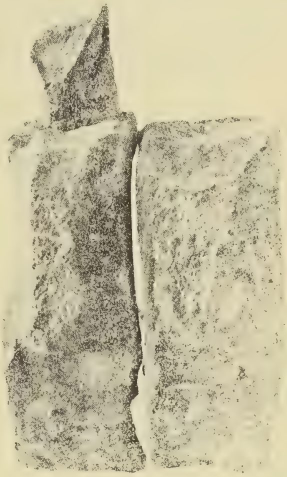
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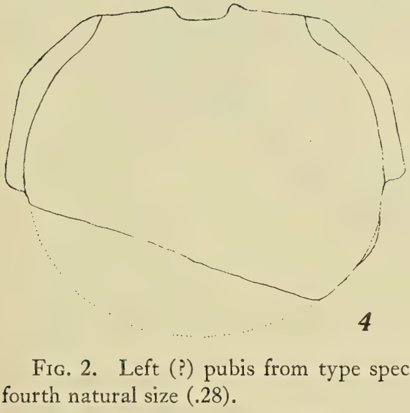
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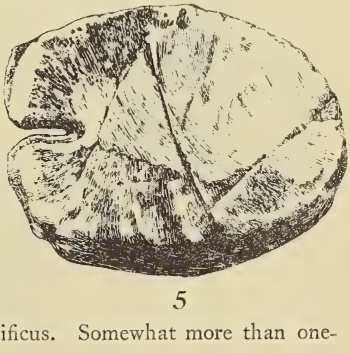
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Fig. 2. Left (?) pubis from type specimen of S. pacificus. Somewhat more than one-fourth natural size (.28).

Fig. 3. **Shastasaurus careyi** n. sp. Posterior cervical or anterior dorsal vertebræ. About one-third natural size.

Fig. 4. Cross-section of posterior of two centra seen in figure 3, showing rudiment of parapophysis. One-fourth natural size.

Fig. 5. **Shastasaurus altispinus** n. sp. Element from anterior margin of a limb. One-half natural size.

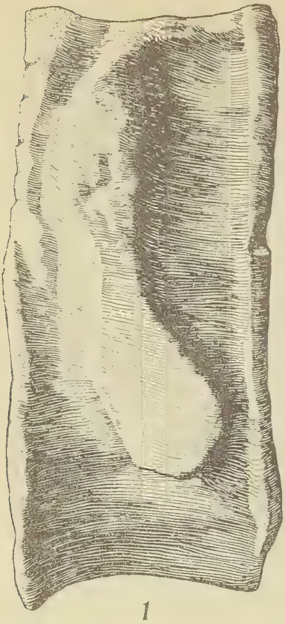

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FIG. 1. Centrum of posterior dorsal vertebra, showing the long, constricted diapophysis separated from the superior articular surface.

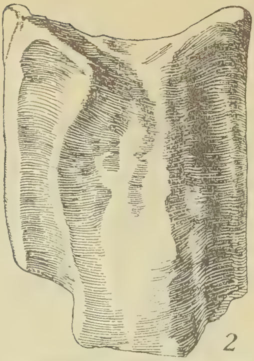

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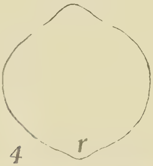
FIG. 2. Centrum of a middle dorsal vertebra. The articular surface of the diapophysis is directly connected with that on the superior side of the centrum.



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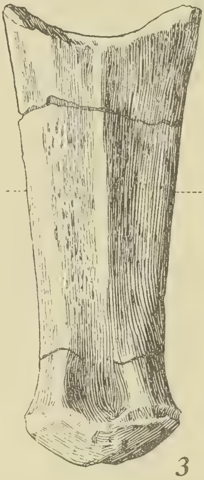

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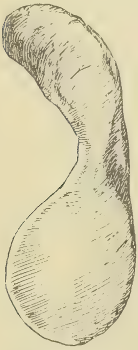
FIG. 3. Posterior view of the spine of a dorsal arch.

FIG. 4. Cross-section of the spine shown in figure 3. The section is taken through the plane indicated by dotted lines on figure 3. *r* indicates posterior side of spine.



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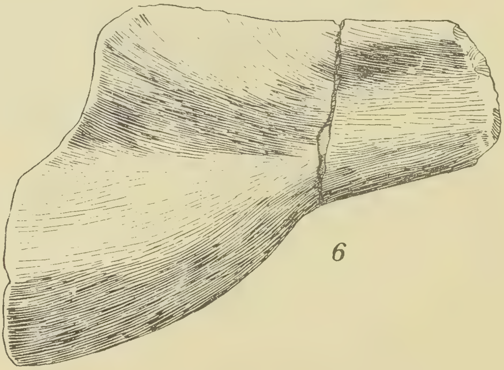

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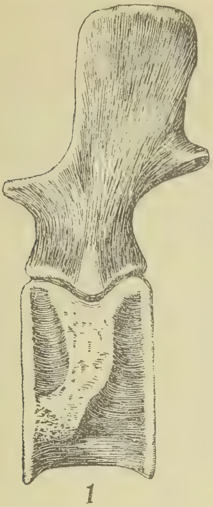
FIG. 5. Articular surface of head of a left dorsal rib.
FIG. 6. Posterior side of head of a right dorsal rib.

Shastasaurus altispinus n. sp.

All figures are from the type specimen, and are represented three-fourths natural size



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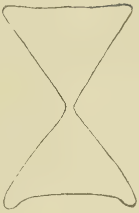

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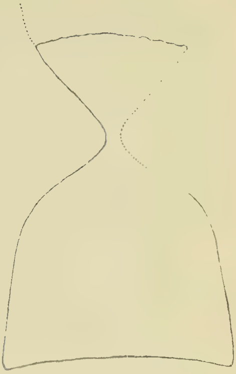
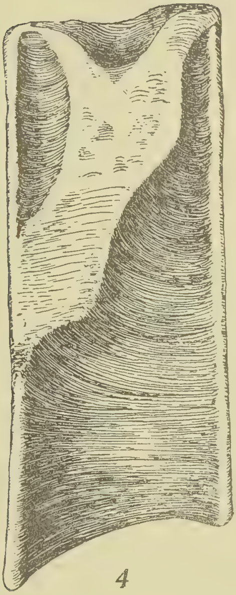


3

FIG. 1. **Cymbospondylus piscosus** Leidy. Anterior dorsal vertebra.

FIG. 2. Antero-posterior section of centrum shown in figure 1.

FIG. 3. **Cymbospondylus (?) grandis** Leidy. Anterior-posterior section of a caudal centrum.



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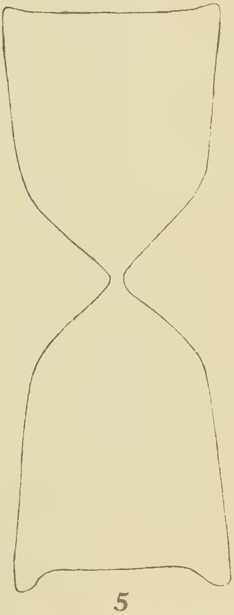

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FIG. 4. **Cymbospondylus petrinus** Leidy. Centrum of an anterior dorsal vertebra. It is probably slightly distorted.

FIG. 5. Antero-posterior section of centrum seen in figure 4, showing flaring articular funnels such as are found in all the individuals of this series.

All figures are from the type specimens, and are represented three-fourths natural size

PRIMITIVE CHARACTERS OF THE TRIASSIC ICHTHYOSAURS

Extensive collections of ichthyosaurian material which have recently been made in the Upper Triassic of California have brought to light a considerable number of species and genera heretofore unknown. Some of these forms exhibit peculiar specializations not found in other representatives of the order. There are, however, a number of primitive characters which are quite strongly marked. These characters are of considerable interest, as they assist somewhat in the attempt to determine the character of the primitive ichthyosaurian.

Leaving out of account such characters as are doubtfully primitive, the following are some of the structures indicating a less marked degree of specialization than is found in the purely aquatic, fish-like ichthyosaurs of the Jurassic:

1. Vertebral centra either perforated or deeply biconcave.
2. Either a larger number of cervical intercentra than in the Jurassic forms or the atlas and axis simpler.
3. Zygapophysial facets of cervical and dorsal vertebræ large, separate, and not usually in the same plane.
4. Neural spines in cervical and dorsal regions thick, sometimes circular in cross-section.
5. Scapula, pubis, and ischium expanded distally, elements of pelvic arch generally robust.
6. Hind limbs sometimes as large or larger than the anterior.
7. Epipodial and phalangeal elements of anterior and posterior limbs generally elongated and showing a median constriction.

Abstract. *Bulletin of the Geological Society of America*, vol. 14, p. 536, March 1904. See short abstract in *Science*, n. s., vol. 17, no. 425, p. 297, February 20, 1903.

NEW ICHTHYOSAURIA FROM THE UPPER TRIASSIC OF CALIFORNIA

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Introduction

In a large collection of Upper Triassic saurian material which has recently been presented to the University of California by Miss A. M. Alexander there are two Ichthyosaurian species differing considerably from any that have been described. Though we are as yet only partially acquainted with their structure, they seem to be generically distinct from all of the known forms. Both specimens were obtained from exposures of the Trachyceras horizon of the Hosselkus limestone occurring a few miles northeast of Winthrop, Shasta County, California.

Relationships and Systematic Position

The Ichthyosauria previously described from the Upper Triassic fauna of California comprise six species placed in the genus *Shasta-*

University of California Publications, Bulletin of the Department of Geology, vol. 3, no. 12, pp. 249–263, pls. 21–24, May 1903.

saurus. So far as the extremities are known, these species are characterized by extreme shortness of the limb elements. The humerus, radius and ulna are wider than long, while the phalanges are circular in outline and ordinarily without lateral notching. The coracoid is antero-posteriorly constricted or pedunculate, the ribs of the middle dorsal region have but one head, and excepting one form (*S. perrini*) the vertebral centra are distinguished by their shortness.

Of the two new types, one (Pls. 21, 22 and 23) is characterized by its elongated limb elements, tridactyle manus, notched or constricted phalanges, shield-shaped coracoid, and long vertebral centra. For this form the new generic and specific name *Leptocheirus zitteli* is proposed.

The second form (Pl. 24) has also the elongated type of vertebral centrum and the slender tridactyle limbs but differs from the other species, so far as known, in possessing dorsal ribs with widely forked heads. Its limbs differ from those of the other new type in that the posterior extremities are larger than the anterior instead of being much smaller. This form has been given the name *Toretocnemus californicus*.

Both *Leptocheirus* and *Toretocnemus* are sharply separated from *Shastasaurus* by their limb structure. The slender propodial, epipodial, and phalangeal elements are wholly different from the greatly abbreviated forms known in *Shastasaurus*. From each other *Leptocheirus* and *Toretocnemus* are distinguished by the character of the rib articulation in the dorsal region and by the difference in the relative size of the limbs.

Both of the new genera, as also *Shastasaurus*, differ considerably from the European *Mixosaurus*.[1] In that genus the limbs have elongated propodial and epipodial segments but are distinguished by being pentadactyle, by having four elements in the first row of the mesopodial segment, and by the articulation of two or more distal carpals on the intermedium. The arches, vertebræ, and dentition are also, as far as known, different from the corresponding structures in the Californian forms. From *Ichthyosaurus* the new genera differ in the form of their pectoral and pelvic arches, the elongation of their epipodial segments, and the constant notching with frequent double notching or shafting of their phalanges.

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[1] See E. Repossi. Il Mixosauro degli strati triasici di Besano in Lombardia. Atti della soc. ital. di scien. natur. Vol. XLI, Fasc. 3, p. 361–372, Tav. VII, IX, Nov., 1902.

Including the forms here described, six distinctly separated groups of Ichthyosaurians designated as genera are now known. These groups may be characterized as follows:

Mixosaurus. Dorsal ribs mainly single-headed. Coracoid pedunculate or with anterior and posterior emargination. Scapula, ischium, and pubis much expanded distally. Interclavicle triangular, with concave borders. Limbs pentadactyle, propodial and epipodial segments elongated. Elements of epipodial segments separated by a wide cleft. Phalanges notched, sometimes with double notching or shafting. Four elements in the proximal row of mesopodial region. Intermedium supporting at least two elements distally. Dentition differentiated.

Leptocheirus. Dorsal ribs, so far as known, single-headed. Coracoid elliptical, without emargination; scapula expanded distally; clavicle broad; interclavicle probably broadly triangular. Limbs tridactyle with a very rudimentary fourth digit. Propodial and epipodial segments elongated. Elements of epipodial segments separated by a wide cleft. Phalanges notched on one or both sides. Three bones in the proximal row of mesopodial segments. Carpus and tarsus with linear arrangement, the intermedium supporting a single element distally.

Shastasaurus. Ribs of dorsal region mainly single-headed. Caudal hypocentra uniting to form long chevron bones. Coracoid pedunculate; scapula, ischium, and pubis much expanded distally. Pubis with deep obturator notch. Elements of pro- and epipodial segments greatly shortened. Radius and ulna separated by a cleft. Ulna considerably smaller than radius.

Cymbospondylus (?) As yet, too imperfectly known for satisfactory generic description.

Toretocnemus. Ribs of the middle or posterior dorsal region with widely forking heads. Caudal hypocentra uniting to form chevron bones. Ischium and pubis much expanded distally. Pubis with obturator foramen. Limbs tridactyle with rudimentary fourth digit, structure in general as in *Leptocheirus.* Posterior limbs larger than anterior.

Ichthyosaurus. Ribs of dorsal region double-headed excepting a few of the most posterior. Coracoid generally pedunculate or with emargination. Scapula, ischium, and pubis narrow. Bones of the epipodial segments greatly shortened, generally in contact along their inner borders. Notching present on only a few phalanges on the anterior border of limb. Number of digits varying from three with a rudimentary fourth to ten. Dentition isodont.

Baptanodon, *Ophthalmosaurus*. Propodial elements articulating distally with three greatly shortened epipodial bones. Dentition considerably reduced.

The subdivision of the order Ichthyosauria into families was attempted by Baur,[2] who set up a family for each of the genera known at that time, *viz.*, Mixosauridæ, Ichthyosauridæ, and Baptanodontidæ. To these three the writer has suggested the addition of the Shastasauridæ[3] as a group sharply distinguished from the others. Repossi's recent paper shows *Mixosaurus* to be much more like *Shastasaurus* than was indicated by previous descriptions. The two genera are, however, distinctly separated, the types of limbs particularly being widely different. Of the two new genera here described *Leptocheirus* is nearer to *Mixosaurus* than to any other of the genera but has throughout a different type of extremity and pectoral arch, while the dentition shows no signs of differentiation. *Toretocnemus* is like *Leptocheirus* in its type of limb, like *Shastasaurus* in the form of its pelvic arch and chevrons, and like *Ichthyosaurus* in the forking of its dorsal ribs.

The question as to how the genera in the order Ichthyosauria should be grouped was one which did not seem difficult to solve when only *Ichthyosaurus*, *Baptanodon*, and *Shastasaurus* were fairly well known and but a small part of the skeleton of *Mixosaurus* had been described. Now that *Mixosaurus* has been carefully described and additional forms have been obtained from the Triassic of California, it becomes a much more difficult matter. To settle it satisfactorily involves a discussion of the primitive characters and the course of evolution of the Ichthyosauria. This is deferred to a study of the subject to appear in a later paper.

DETAILED DESCRIPTION OF NEW GENERA AND SPECIES

Leptocheirus, New Genus

Caudal vertebræ elongated. Dorsal ribs single-headed. Coracoid shield-shaped, much elongated antero-posteriorly, without anterior or posterior emargination. Extremities with three slender

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[2] G. Baur, Ueber den Ursprung der Extremitäten der Ichthyopterygia, Ber. d. XX Versam. d. Oberhein. Geol. Ver. Vol. XX, p. 3.

[3] Bull. Dept. Geol. Univ. Calif., Vol. 3, p. 87.

digits and rudiment of a fourth. Anterior limb much larger than posterior. Elements of the propodial and epipodial segments of anterior and posterior limbs much longer than broad. Epipodial bones separated by a wide cleft. Bones of first and third rows of the mesopodial, metapodial, and phalangeal regions all notched on one or both sides. Carpus and tarsus with linear arrangement, three elements each in the proximal and distal rows, intermedium articulating distally with but a single bone. Dentition isodont, conical teeth set in open grooves.

Leptocheirus zitteli n. sp.

PLS. 21, 22, AND 23

The type specimen (No. M 8099, University of California Palæontological Museum) is represented by the lower half of a skull with a part of the dentition, the complete pectoral girdle, both anterior limbs, and numerous fragmentary ribs, vertebræ, and abdominal ribs. It was discovered by Miss A. M. Alexander in the Trachyceras zone of the upper Triassic limestones at the Cove near Madison's Ranch on Squaw Creek, Shasta Co.

Vertebræ and ribs.—The only well-preserved vertebra present is an anterior caudal (Pl. 23, fig. 4) with the following dimensions: length 14 mm., height 22 mm., greatest width 24 mm. The end faces are very deeply concave, sloping sharply from the periphery and almost meeting in the center. The diapophyses are small but have considerable lateral projection. The articular surfaces for the reception of the lower arches are situated on rather prominent apophyses. The centrum is hexagonal in cross-section, the inferior surface and the lateral areas above and below the diapophyses being flat or slightly concave.

The *ribs* are very imperfectly preserved and only one specimen was found in which the form of the head and shaft can be seen distinctly. The single head is twisted backward and both sides of the shaft are grooved, the posterior more deeply than the anterior. The form of this rib is similar to that in the dorsal region of *Shastasaurus perrini*. A great many of the *abdominal ribs* are present in their original positions. They are in five linear series like those of *Ichthyosaurus*.

Anterior arch.—Excepting the clavicles and the inter-clavicle, which had slipped forward a short distance, the bones of the pectoral girdle were all in their natural positions, with the limbs in place on each side. The *coracoids* (Pl. 21, fig. 2) are very much expanded antero-posteriorly. Their diameter measured in this direction is twice the length of that taken transversely. Their form is roughly elliptical. The anterior and posterior ends are gently-rounded and there is no trace of an anterior or posterior emargination. There is no pedunculation of the portion articulating with the humerus and scapula as in *Shastasaurus* and *Mixosaurus*, though the proximal portion is considerably thickened. The portion next the median line is considerably thickened by a high ridge running obliquely forward. The *scapulæ* (Pl. 21, fig. 2) are short and broad, having the general form seen in *Shastasaurus*. The articular surface is curved so as to form two fairly distinct facets for the coracoid and humerus. The anterior hook is shorter and the notch below it not so well marked as in *Shastasaurus osmonti* or *alexandræ*. As the posterior angle of the upper margin is very thin, it probably did not extend far beyond the limits given in the figure and was therefore shorter than in *S. osmonti*.

The *clavicles* (Pl. 21, fig. 1) are represented by two heavy, broad bars meeting, or possibly overlapping, on the median line in front of the coracoids. The ends next the scapulæ are broken away so that the total length of these elements can not be determined. The ends next the median line are considerably broadened and are concave on the posterior side. As far as can be determined the clavicles are much like those of *Shastasaurus alexandræ* and *osmonti*.

An elongated, triangular bar, shaped somewhat like a boomerang, stretches across the median line below the contact of the clavicles and possibly represents the *interclavicle* (Pl. 21, fig. 1, Ic and Ic′). One-half of the triangle is perfectly preserved. The angle on the other side has been broken away, but had probably a form similar to the part present. The obtuse angle on the convex side of the bone may represent the median stem of the interclavicle in *Ichthyosaurus*. If this element is entire the posterior angle or median stem is much more reduced than in any other known Ichthyosaurian.

MEASUREMENTS

Coracoid	
Antero-posterior diameter	72 mm.
Transverse diameter	35
Greatest thickness at proximal end	12.5
Greatest thickness on distal margin	15

Scapula	
Length	40 mm.
Thickness at proximal end	11
Width at proximal end	[4]19
Clavicle	
Width at end next median line	16
Width in middle of shaft	11

Anterior limbs (Pl. 22, fig. 1).—In agreement with the generally elongated type of the limb, the *humerus* is considerably longer than broad. The distal end is wider than the proximal, having a transverse diameter equalling two-thirds the length of the bone. The trend of the anterior border is nearly at right angles to that of the distal margin, while the posterior border slopes backward. This means that the posterior side of the limb would receive a little less power than the anterior side, a fact that might have some influence in determining the location of reduction in the phalangeal portion of the limb. In the middle of the anterior margin is a sharply cut notch which is opposite the deepest part of a much broader indentation of the posterior side. This constriction of the middle of the humerus clearly represents the original shaft of the bone. Its presence here helps to explain the occurrence of a similar constriction in the more specialized humerus of *Shastasaurus*. A prominent ridge on the upper side of the proximal end is opposite a much larger elevation corresponding to the pectoral ridge on the inferior side. Both prominences extend to about the middle length of the humerus. A narrow ridge on the posterior distal angle of the upper side is opposite a similar elevation on the ulna. The radial and ulnar borders are both sharply concave as in *Ichthyosaurus*.

The *radius* has exactly one-half the length of the humerus. The anterior border is nearly straight, showing only a faint indentation near the middle. The posterior border is deeply concave. The surface of contact with the radiale takes up nearly the whole of the distal end. The contact with the intermedium is only along the posterior angle.

The *ulna* has a deeply concave anterior border, and as in *Mixosaurus* shows no emargination on the posterior side. The facets for the intermedium and the ulnare are of nearly the same length. A low triangular ridge is present near the posterior proximal angle.

The *carpus* and *metacarpus* consist of three linear series of three bones each. The radiale is a little wider proximally than the ulnare, and in consequence the intermedium articulates principally with the ulna. The intermedium and the other two ossicles of the middle linear series have entire margins. All the elements of the two outer series are notched on the margins next the lateral borders of the limb. In both right and left limbs the metacarpal of digit one is deeply notched on both sides.

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[4] Approximate.

The *phalangeal* region consists of three well developed digits and the merest vestige of a fourth. There are seven phalanges in digits one and three, and eight in the middle finger. The terminal phalanges are exceedingly small and simple and it is not probable that more than one or two have been lost from this specimen.

What may be considered as a rudimentary or perhaps as an incipient digit four is represented in both right and left limbs by two very small ossicles. These elements are opposite the first phalanx in one limb and opposite the first and second in the other. One or two additional ossicles may have been present in this row but a careful search has failed to reveal them.

Excepting phalanx one of digit two and two very minute rounded ossicles at the distal end of the paddle, all of the phalanges are sharply notched. Half of the phalanges in digits one and three are notched on both sides; the remaining ones are cut in on the outer border only. In digit two the notching is, for some unknown reason, always on the posterior side of the phalanges. The presence of the double notching on many of the phalanges, occurring as it does with greater axial length than is found in these elements in the later groups of the Ichthyosauria, can hardly be interpreted otherwise than as an indication that the phalanges were originally even longer than we find them here and that their middle or shaft portions were considerably constricted as in the normal phalanx of a shore or land reptile.

MEASUREMENTS

Humerus	
Length	61 mm.
Width at proximal end	34
Width at distal end	41
Width at notch	22
Thickness through pectoral ridge	20

Radius	
Greatest length	31 mm.
Width, proximal and distal	20
Width, median	16.5
Ulna	
Greatest length	31
Width, proximal and distal	20.5
Width, median	18
Radiale	
Length	15
Width	14.5
Distal carpal one, length	11.5
Metacarpal one, length	10

Posterior limbs (Pl. 22, fig. 2).—The posterior limb is much smaller than the anterior, the parts present indicating that its total length was about one-third shorter. This paddle is also of the tridactyle type but the fourth digit is a little larger than that indicated in the anterior limb. The femur is much smaller than the humerus and has a much more slender median or shaft region. The tibia and fibula were both considerably longer than broad and each shows a marked median constriction, the notches being very deep on the inner side. The tibia is somewhat broader than the fibula.

The tibiale is imperfectly preserved. The anterior margin is not shown and it is not possible to determine whether it was notched. The intermedium is imperfect as is also the fibulare. It is not possible to state whether the latter was notched on the posterior side. Distal tarsal two is well preserved and has entire margins. Distal tarsal three is deeply notched posteriorly. In the metapodial region numbers two and three are preserved. Like the corresponding element of the anterior limb, number two has entire margins. Number three shows a deep median constriction like that in number one of the corresponding region of the anterior limb.

In the phalangeal region, the arrangement and form of the elements is much the same as in the anterior limb. The rudimentary fourth digit is represented by four small ossicles situated immediately behind the mesopodial and metapodial regions.

MEASUREMENTS

Femur	
Width of distal end	[5]30 mm.
Width of narrowest portion of shaft	18

[5] Approximate.

Tibia	
Length	19 mm.
Width	16
Distal tarsal three	
Length	9
Width	7
Metatarsal three	
Length	7
Width	5.5

Skull (Pl. 23, figs. 1, 2, and 3).—Of the cranial portion only the maxillary, jugal, lachrymal, and postorbital are preserved in such form that they can be satisfactorily studied. The relations of these elements are not markedly different from those in *Ichthyosaurus.* In a cross-section of the middle portion of the skull as it appears on this specimen there are two palatal bones, probably the palatines and a median element having the appearance of the vomer. In each orbit there is a large portion of a sclerotic ring composed of plates of considerable size.

The mandible is constructed much like that of *Ichthyosaurus*, with the exception that the supra-angular is somewhat larger, taking up nearly the whole of the outer side back of the middle of the orbit. The angular is visible on the outer side of the jaw only as a very narrow strip near the posterior end. A cross-section of the mandible taken below the anterior end of the lachrymal (Pl. 23, fig. 3) shows a very large spenial extending below the supra-angular, and a saddle-like section of the dentary resting upon the supra-angular and overlapping it on the outside.

In a section at the posterior end of the mandible (Pl. 23, fig. 2) there are shown the supra-angular, angular, and a large element (*ar*) which can hardly represent anything other than the articular. This seems to be an elongated bone of considerable size. In addition to these there is possibly a fourth element (x), which resembles somewhat a bone doubtfully determined as corresponding to the coronoid in *Shastasaurus alexandræ.* This element is very indistinct and may not be separate from the angular.

Dentition.—Though many scattered teeth supposed to belong to Ichthyosaurians have been found in the Californian Triassic, this is the first specimen to show the dentition in place in the jaws. As is shown in Plate 23, figure 1, the slender conical teeth are very numerous and closely crowded. As in *Ichthyosaurus*, they are inserted in rather shallow, open grooves (Pl. 23, fig. 3). There is no evidence that bony partitions separate the teeth transversely as in *Mixosaurus*. As the maxillary teeth are conical the dentition is evidently isodont. What appear to be short and broad teeth near the posterior end of the series in Plate 23, figure 1, are individuals which could be only partly exposed in preparation, owing to their turning inward. As the teeth are softer than the matrix it has not been possible to expose their surfaces satisfactorily, and the structure could be studied only in cross-section. So far as can be seen, they are not materially different from the teeth of *Ichthyosaurus*.

Toretocnemus, New Genus

Vertebral centra elongated. Neural arches with lateral ridge, not greatly thickened. Middle dorsal ribs with widely forking heads articulating on small and widely separated diapophyses and parapophyses. Caudal vertebræ with single-headed ribs and Y-shaped lower arches. Limbs tridactyle, with a rudimentary fourth digit. Propodial and epipodial segments elongated. Elements of epipodial segments separated by a wide cleft. Posterior limbs equaling or excelling the anterior in size. Ilium long and slender. Pubis very broad, with obturator foramen.

Toretocnemus californicus n. sp.

Pl. 24

This species is represented by a specimen (No. M 8100 University of California Palæontological Museum) embedded in a slab which had been weathered in such a manner that a large portion of the skeleton was carried away. There remain nearly all of the ribs, the middle and posterior dorsal and the anterior caudal vertebræ, the pelvic arch, both hind limbs, and the right anterior limb. The type specimen was discovered by Miss A. M. Alexander in the Upper Triassic limestones at Bear Cove, three miles north of Brock's Ranch, on Pitt River, Shasta County.

Vertebræ and ribs.—About thirty *vertebræ* are present, two-thirds of the number being behind the pelvic arch. The centra are all deeply biconcave and have a length equal to about half their height. On the most posterior vertebræ the upper arches are about a third higher than the centra and have rather thin, sharply recurved spines. The zygapophyses are here represented by notches. The diapophyses on these vertebræ are a trifle below the middle of the centrum. Immediately behind the pelvis the upper arches become higher, broader, and more nearly erect and the zygapophyses are better developed. In this region the diapophyses are low down on the sides of the centra and are considerably elongated vertically by swinging downward and forward to the anterior margin. Below the contact of two of the caudal centra there is a V-shaped lower arch like those known in *Shastasaurus perrini.*

Near the middle of the dorsal region the diapophyses are small and round and lie above the middle of the side of the centrum, while prominent parapophyses with backwardly directed facets are present low down and nearer the anterior margin (Pl. 24, fig. 4).

MEASUREMENTS

Middle dorsal centrum, length	11 mm.
" " " height	[6]14.5
Anterior caudal centrum, length	10
" " " height	13

The *ribs* associated with the dorsal vertebræ described above have broadly forked heads, the two articular surfaces being separated by a strong notch (Pl. 24, fig. 4). A prominent ridge begins behind the point of separation of the two heads and runs along the upper portion of the anterior side of the shaft as in *Shastasaurus.* A little farther back in the column the two heads are still distinctly separated, but the notch between them is much shallower. Numerous cross-sections of ribs show both the circular section such as is obtained near the end and the constricted section obtained in the doubly grooved middle or proximal portion of the shaft in *Shastasaurus.*

Posterior arch (Pl. 24, fig. 3).—The entire pelvic arch lay below the vertebral column, immediately in front of what are recognized as the anterior caudal vertebræ. Although the girdle is moved from its normal position with relation to the vertebral column, the elements are in very nearly their natural positions with relation to each other. The ilia are considerably longer than the ischia and pubes, and are much more slender and longer than in *Shastasaurus perrini.* The ischia are also narrower than in *S. perrini.* In the extremely broad pubes the obturator notch of *Shastasaurus* is represented by an obturator foramen.

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[6] Approximate.

MEASUREMENTS

Ilium	
Length to broken distal end	29 mm.
Ischium	
Greatest length	22
Greatest width	14.5
Pubis	
Greatest length	23.5
Greatest width	22

Posterior limbs (Pl. 24, fig. 1).—Both of the posterior extremities lie near the pelvic arch. The proximal portion of each limb had been beautifully exposed by weathering, but unfortunately the phalanges are missing.

The shaft of the *femur* is constricted and twisted in the middle, and the expanded ends are turned so as to cut each other at an angle of about seventy-five degrees. The main projection of the twisted proximal end beyond the plane of the distal end seems to be toward the upper side, forming a great trochanteric ridge. The tibial and fibular borders are both markedly concave.

The tibia and fibula have about half the length of the femur, and both are longer than wide. The *tibia* differs from the fibula in having the anterior and posterior borders of about the same length. The proximal end is gently rounded, corresponding to the concave articular surface of the femur. The articular facet for the tibiale is long and is normal to the long axis of the bone. The facet for the intermedium is small and oblique. The middle or shaft portion is considerably constricted, the indentation of the anterior margin being less than that on the posterior border.

The *fibula* is somewhat narrower than the tibia. The straight posterior border is much longer than the deeply emarginate anterior side. The proximal margin is much more oblique to the axis than in the case of the tibia. The articular facets for the intermedium and the fibulare are of about equal length and are both oblique.

In the *tarsus* the tibiale and distal tarsal one have a quadrate form and are deeply notched in the middle of the anterior border. The pentagonal intermedium, the square distal tarsal two immediately below it, and the similarly formed metatarsal two show no emargination. The fibulare possesses a small notch on the outer border. On its distal side there is a large facet for distal tarsal three and a smaller, oblique one on which there probably rested an ossicle belonging to a fourth digit. Similarly there are two facets on the distal end of distal tarsal three, one for metatarsal three and an oblique outer facet of the same size for a metatarsal four. Distal tarsal three has no emargination on the outer or posterior border such as occurs in *Leptocheirus* on the outer side of the carpals along the borders of the paddles. This is evidently due to the fact that the lateral border was here partially or entirely covered by a series of elements belonging to a rudimentary fourth digit.

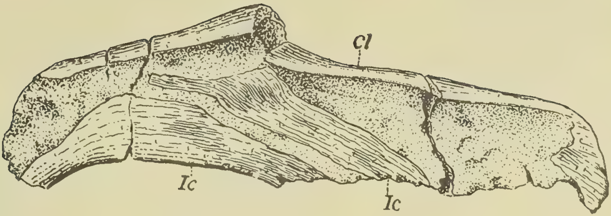
MEASUREMENTS

Femur	
Length	32.5 mm.
Width of proximal end	16
Width of distal end	24
Thickness at twist, parallel with plane of distal end	8
Thickness of proximal end	11
Tibia	
Length	15
Width, proximal	13
" notch to notch	8
" distal	12
Fibula	
Greatest length	18
Width, median	9.5
" distal	12
Fibulare	
Length	8
Width	7.5
Distal tarsal one	
Length	6
Width	7

Anterior limbs (Pl. 24, fig. 2).—The anterior limb has unfortunately been weathered on one side so that the proximal and posterior portions of the humerus and the part of the manus behind the second digit are gone. So much of the limb as is present resembles considerably the type of anterior extremity found in *Leptocheirus*. The width of the radius appears to be slightly greater, its anterior notch deeper, and the notching of the metapodial and phalangeal bones seems to be carried farther than in *Leptocheirus zitteli*. In digit one the metacarpal and all of the phalanges are notched on both anterior and posterior sides. In digit two phalanx one has a deep posterior notch, while two and three are notched on both sides.

MEASUREMENTS

Radius	
Greatest length	15 mm.
Width, proximal and distal	12
" between notches	9
Radiale	
Length	8
Width, proximal	8.5
" at notch	6.5
" distal	7.5



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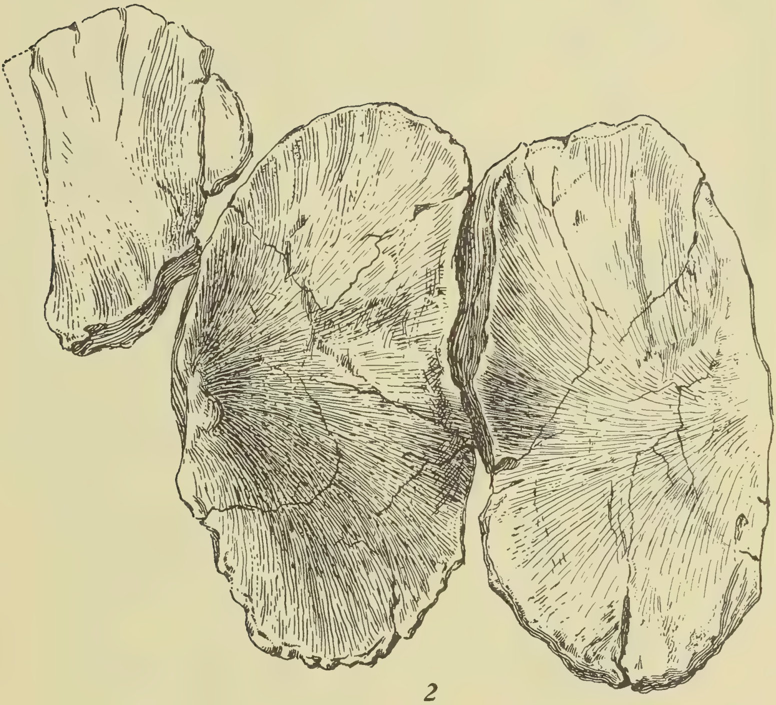


2

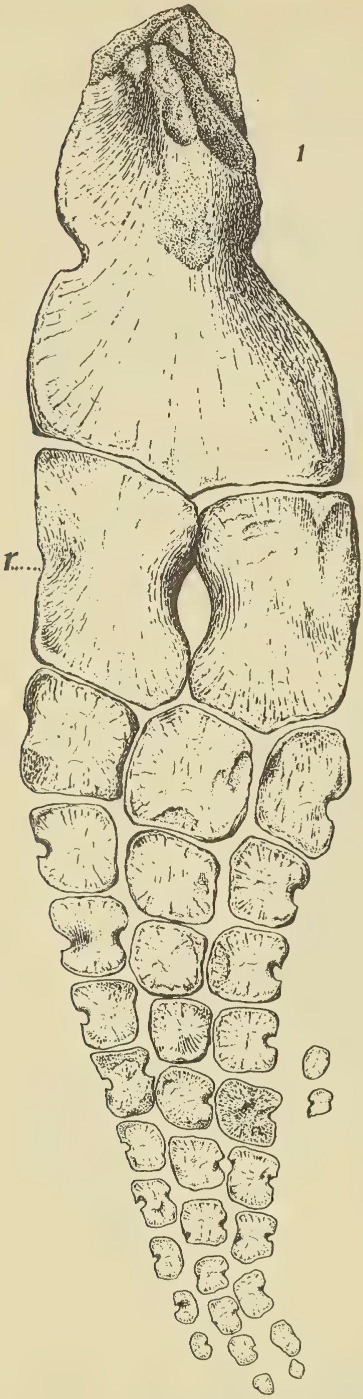
Leptocheirus zitteli n. gen. and sp.

Figures reproduced natural size from the type specimen

FIG. 1. Clavicles (cl) and probable interclavicle (Ic and Ic′). The interclavicle has been separated into two fragments by a crack in the matrix.

FIG. 2. Inner side of the coracoids and the left scapula.

1



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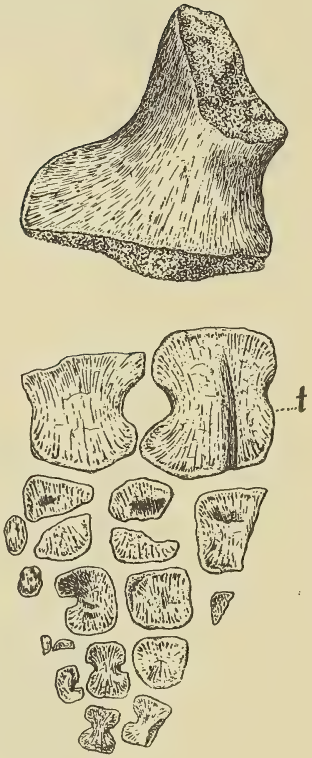
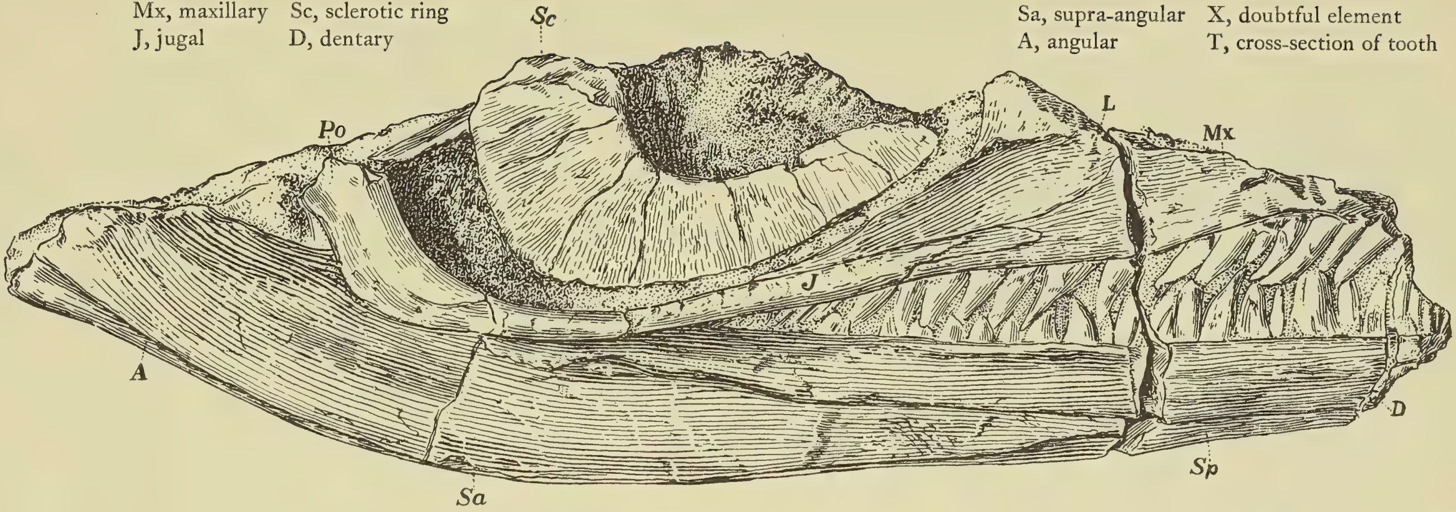


Leptocheirus zitteli n. gen. and sp.

Figures reproduced natural size from the type specimen

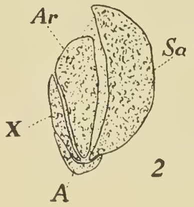
FIG. 1. Superior side of left anterior limb. *r*, radius.
FIG. 2. Posterior limb. *t*, tibia.

L, lachyrmal
Mx, maxillary
J, jugal
Po, postorbital
Sc, sclerotic ring
D, dentary
Sp, spenial
Sa, supra-angular
A, angular
Ar, articular
X, doubtful element
T, cross-section of tooth



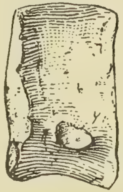
1

Right side of skull



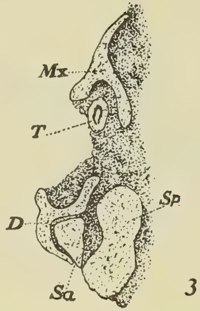
2

Cross-section of posterior portion of the lower jaw, taken above the point marked *A* on the lateral view of the skull.



4

Lateral view of an anterior caudal centrum

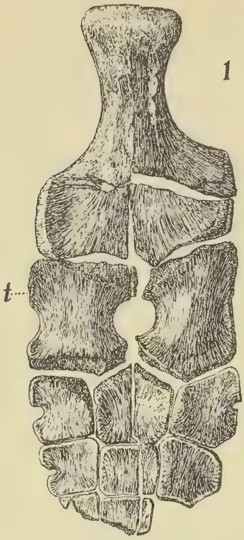


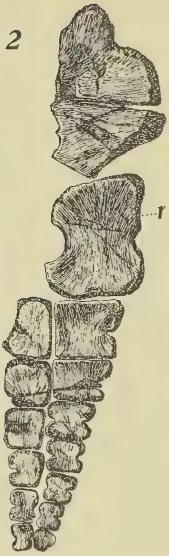
3

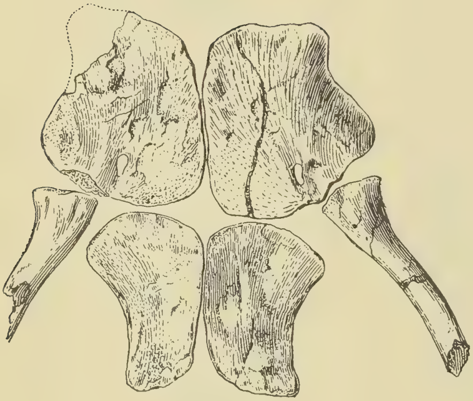
Cross-section of the upper and lower jaws, taken at the break immediately behind the point marked *Sp* on the lateral view of the skull.

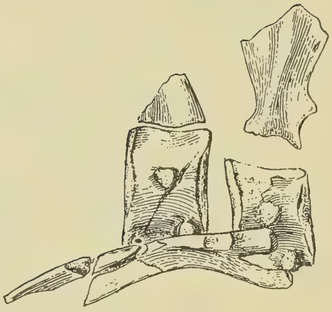
Leptocheirus zitteli n. gen. and sp.

Figures reproduced natural size from the type specimen









Toretocnemus californicus n. gen. and sp.

Figures reproduced natural size from the type specimen

FIG. 1. Inferior side of right posterior limb. *t*, tibia.
FIG. 2. Right anterior limb. *r*, radius.
FIG. 3. Pelvic arch.
FIG. 4. Middle dorsal vertebræ and a rib from the same region.

RECENT LITERATURE ON TRIASSIC ICHTHYOSAURIA

Within the past few months two important contributions have been made to our knowledge of the Triassic Ichthyosauria of the Eastern Hemisphere. The more extensive of these papers is one by Dr. E. Repossi,[1] giving the long-desired exact description and illustration of the material upon which Baur based the genus *Mixosaurus*. In this paper the statements of Baur concerning the primitive characters of this genus are strongly supported and many previously unknown and even unsuspected characters have been brought to light.

One of the most important contributions made by Repossi is the description of the pectoral and pelvic arches. These are quite unlike those of any Post-Triassic form of the order, but show a strong similarity to the corresponding structures in the Californian genus *Shastasaurus*. All of the elements excepting the ilium and clavicle are much broader and more robust than in *Ichthyosaurus*. The inter-clavicle is more nearly triangular than T-shaped and is hence more stegocephalian. The scapula, like that of *Shastasaurus*, has more of a mosasaurian than of an ichthyosaurian aspect.

Beautifully preserved specimens show the limbs to be pentadactyle with elongated epipodial bones and notched or sometimes shafted phalanges. A peculiar feature is found in the presence of four elements in the proximal row of the carpus and tarsus. Were it not for the character of the specialized mesopodial region, these limbs might well be considered as the primitive types from which the limbs of *Ichthyosaurus* were derived. The limb structure differs considerably from the types found in the Californian genera, both in the number of digits and in the character of the mesopodial region.

Another interesting discovery is the fact that the dorsal ribs of

Science, n. s., vol. 18, no. 453, pp. 311–312, September 4, 1903.

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[1] Em. Repossi. 'Il Mixosauro degli strati triasici di Besano in Lombardia,' *Atti della soc. ital. di scien. natur.*, Vol. XLI., Fasc. 3, p. 361–372 tav. VIII., IX. Novemb., 1902.

Mixosaurus are mainly single-headed. Those who have concerned themselves with this group seem generally to have taken for granted a double rib articulation.

A second paper of interest dealing with Triassic Ichthyosauria is one by N. Yakowlew on 'New Finds of Triassic Saurians in Spitzbergen.'[2] One of the specimens here described was found near the locality at which the type of Hulke's *Ichthyosaurus polaris* was discovered by Nordinskiöld, and as it resembles *I. polaris* in the size and general form of the vertebræ, it has been referred to this species. A posterior dorsal vertebra which has been figured is shown to differ from *Ichthyosaurus* in possessing a single broad apophysis for the articulation of the rib. This species is, therefore, placed by Yakowlew in the genus *Shastasaurus*. The vertebra is certainly very similar to some of the posterior dorsals of *Shastasaurus*. After a study of Hulke's descriptions and measurements of the type material, the writer has already expressed the opinion[3] that a careful examination would show it to belong in the Californian genus.

In this paper the valuable suggestion is made by Yakowlew that the ribs of the Ichthyosauria were primitively single-headed and that the double-headed form has been produced by more complicated and stronger movements of the ribs, causing disappearance of the middle portions of the rib heads and of the corresponding parts of the lateral apophyses of the vertebræ. In a later article[4] written mainly in review of Repossi's paper on *Mixosaurus*, Yakowlew expresses the opinion that the double-headed character appeared first in the posterior portion of the dorsal region owing to the more vigorous movement of that portion of the body. It is difficult to reconcile this theory with the fact that in *Ichthyosaurus* the ribs tend to be single-headed toward the base of the tail and double-headed anterior to it, and that in *Shastasaurus*, which had also a great sculling tail, the ribs are all single-headed excepting a very few immediately behind the head.

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[2] 'Neue Funde von Trias-Sauriern auf Spitzbergen,' *Verhand. der Kais. Russ. Mineralog. Ges.*, Bd. XL., S. 179–202.

[3] 'Triassic Ichthyopterygia of California and Nevada,' p. 88.

[4] 'Einige Bemerkungen ueber die triassischen Ichthyosaurier.' *Verhand. der Kais. Russ. Mineralog. Ges.*, Bd. XL., Lief. II.

Concerning Yakowlew's suggestion that the single-headed rib is the primitive type in this order, it is certainly a significant fact that it seems to occur frequently in the Triassic ichthyosaurs. We should not forget, however, that the oldest representative of the order which has been described, viz., Quenstedt's *atavus*, from the lower Muschelkalk, is said to have a double articulation and is possibly not to be referred to *Mixosaurus*, as has been generally supposed. Recent discoveries have shown the existence also in the Californian Triassic fauna of a form (*Toretocnemus*[5]), in which the middle dorsal ribs are as widely forked as in *Ichthyosaurus*. Again, it appears that in *Shastasaurus* the double articulation in the anterior part of the column is not formed by reduction of the middle portions of simple lateral apophyses. From the atlas to the anterior dorsal region the diapophyses are gradually increased in height and the parapophyses reduced till the latter are mere points some distance below the lower ends of the diapophyses. The lateral apophyses of the dorsal region, therefore, correspond to the diapophyses in the cervical region. If the double articulation in the neck region is secondary it would appear to have required the *addition* of a lower rib head and a parapophysis. There appears, therefore, to be still a chance that the double articulation is primitive in this group, and it may be well to withhold final judgment till we have a better acquaintance with the structure of the vertebral column as a whole in the later Triassic forms, and particularly till we know more about the Middle Triassic representatives of the group.

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[5] See *Bull. Geol. Dept. Univ. of Calif.*, Vol. 3, No. 12, p. 260.

THE TYPES OF LIMB STRUCTURE IN THE TRIASSIC ICTHYOSAURS

The Types of Limb Structure in the Triassic Ichthyosaurs: JOHN C. MERRIAM, Berkeley, California. To be printed in *American Journal of Science.*

The limb structure in the Triassic ichthyosaurs shows generally a much stronger resemblance to the type of extremity found in the primitive shore forms of the reptilia than is seen in the Jurassic forms. The limbs of Triassic ichthyosaurs show as great a degree of differentiation as is found in the later types. Two fairly definite lines of evolution are noticeable in the paddle structure of the Ichthyosauria, one leading to the broad-paddled Latipinnati, the other leading to the Californian Triassic genera and to the narrow-paddled Longipinnati.

Abstract of paper presented at meeting of Section F (Zoology), American Association for the Advancement of Science, St. Louis, December 1903. *Science*, n. s., vol. 19, no. 475, p. 218, February 5, 1904.

A NEW GROUP OF MARINE REPTILES FROM THE UPPER TRIASSIC OF CALIFORNIA

A New Group of Marine Reptiles from the Upper Triassic of California: JOHN C. MERRIAM, Berkeley, California. To be printed in 'Publications' of the University of California.

Marine saurians with abbreviated limbs and slender, elongated snout. External nares median. Temporal arcades slender. Dentition heterodont, posterior teeth flat, anterior teeth slender, conical. Elongated vomer with two rows of flat teeth. Pterygoid (?) with numerous slender conical teeth. This group stands in somewhat the same relation to the typical Rhynchocephalia as that which the Pythonomorpha bear to the Lacertilia. Evidently derived from primitive land or shore rhynchocephalians, it has taken somewhat the same course in evolution as that followed by the ichthyosaurians and parasuchians. From both of these groups it differs very considerably in the structure of the vertebræ, limbs and skull. It is sharply separated from both by the characters of dentition. The name Thalattosauria has been used to designate this group.

Abstract of paper presented at meeting of Section F (Zoology), American Association for the Advancement of Science, St. Louis, December 1903. *Science*, n. s., vol. 19, no. 475, p. 218, February 5, 1904.

A NEW MARINE REPTILE FROM THE TRIASSIC OF CALIFORNIA

In the collections of marine Triassic reptiles at the University of California there are a number of specimens representing a heretofore unknown form of swimming reptile. In advance of a more complete discussion of the structure and affinities of this group, the following description of the type specimen is presented.

Thalattosaurus alexandrae, new gen. & sp.

Figure 1

Cranium elongated, with slender snout. External nares separated and not far in front of the orbits. Dentigerous portion of the premaxillaries elongated but shorter than the maxillaries. Premaxillaries and maxillaries sculptured on the external surface.

Vomers with two rows of flat, button-like teeth. Pterygoids with four or more rows of curved, conical teeth. Palatines not known to be dentigerous. Teeth of the premaxillaries and of the anterior end of dentary slender conical. Posterior part of dentary and probably of maxillaries with button-like, flat or only slightly tuberculate teeth.

Vertebrae amphicoelous, neural spines slender. Dorsal ribs single-headed. Coracoid reniform, elongated antero-posteriorly. Scapula narrow. Humerus short, much expanded distally. Radius and ulna about half the length of the humerus; radius with median constriction. Pelvic arch robust, inferior elements not plate-like.

The type specimen (No. $\frac{1013}{9085}$ Pal. Mus. Univ. Cal.) was found in the Trachyceras beds of the Hosselkus limestone in the Upper Triassic of Shasta County. It includes the anterior two-thirds of the skull and a portion of the temporal region; also parts of over thirty vertebrae, numerous fragmentary ribs, the principal elements of the pectoral and pelvic arches and a considerable portion of an anterior limb.

This species is named in honor of Miss A. M. Alexander, who has

University of California Publications, Bulletin of the Department of Geology, vol. 3, no. 21, pp. 419–421, October 1904.

not only contributed generously to the financial support of the work on the vertebrates of the marine Triassic but was herself the discoverer of the type specimen furnishing the largest part of our information concerning the group.

In its fundamental outlines, the skeletal structure in *Thalattosaurus* is strongly suggestive of the Rhynchocephalia, but like many of the so-called rhynchocephalian groups it differs so far from the typical forms represented by *Sphenodon*, *Homaeosaurus*, etc., that it can not be included in the same ordinal division. It is likewise so different from all of the other described reptilian families and orders that it must be given an independent position. The family name *Thalattosauridae* and the ordinal name *Thalattosauria* are therefore used to express its position in the scheme of classification.

Recently a number of groups possessing rhynchocephalian characters have been tentatively brought together as orders in a superorder, Diaptosauria, by Osborn.[1] Although diaptosaurian in one sense simply spells *primitive*, this classification serves to emphasize the distinct kinship certainly shown by many of these forms. For the present the Thalattosauria may be placed in the superorder Diaptosauria, though it is doubtful whether it will be retained in that division or even whether the Diaptosauria can hold together when the various forms included in it become better known. With increased knowledge of the Triassic reptiles, it will naturally become increasingly difficult to determine whether or not some of the orders classed with the Diaptosauria are more deserving of a position in that group than, for example, the rhynchocephaloid Parasuchia having an independent position.

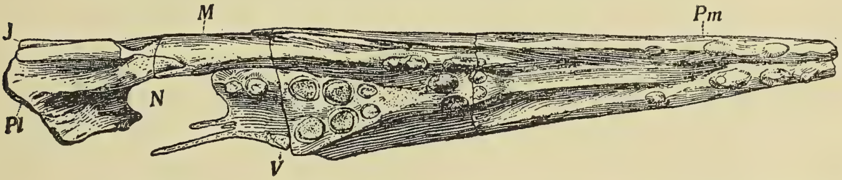

FIG. 1. *Thalattosaurus alexandrae.* Inferior side of the anterior portion of the cranium. *M*, maxillary; *Pm*, premaxillary; *V*, vomer; *Pl*, palatine; *J*, jugal; *N*, narial opening. × ½.

Inside the Diaptosauria the closest affinities of the Thalattosauria are with the Proganosauria and Choristodera. From both groups they differ more widely than these two differ from each other. In many respects, particularly in limb structure, the Thalattosauria represent more highly specialized aquatic forms than the other two orders.

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[1] H. F. Osborn. The Reptilian Subclasses Diapsida and Synapsida and the Early History of the Diaptosauria. Mem. Am. Mus. Nat. Hist., Vol. 1, Part 8, 1903.

Outside of the Diaptosauria there are noticeable resemblances to the Parasuchia and to the Lacertilians. The common characters are, however, almost without exception, primitive or rhynchocephalian characters which we find persisting in the Parasuchia and Squamata.

Some of the most interesting points of resemblance to known forms shown by *Thalattosaurus* are found in its similarity in parts of the skull to *Proterosuchus* Broom, from the Karoo Beds. This form is referred to by Broom as "... a primitive Rhynchocephalian which shows a considerable degree of specialization along the line which gave rise to the early Crocodiles and Dinosaurs." Here, as in other groups compared, the skull structure shows important differences. Judging from these differences and from the occurrence of *Proterosuchus*, we may expect that the limbs in that form will prove to have a structure very different from that in *Thalattosaurus*, and will tend rather toward the crocodilian type. While showing noteworthy affinities, it would be impossible to bring *Proterosuchus* and *Thalattosaurus* nearer to each other than related orders of the Diaptosauria could come.

A NEW GROUP OF MARINE REPTILES FROM THE TRIASSIC OF CALIFORNIA

In the collections of marine Triassic vertebrates at the University of California there are a number of specimens representing a heretofore unknown form of swimming Reptile. This form has been made the type of a new genus and species having the following characters.

Thalattosaurus Alexandræ, n. gen. n. sp.

Cranium elongated, with slender snout. External nares separated and not far in front of the orbits. Dentigerous portion of the premaxillaries elongated but shorter than the maxillaries. Premaxillaries and maxillaries sculptured on the external surface.

Vomers with two rows of flat, button-like teeth. Pterygoids with four or more rows of curved, conical teeth. Palatines not known to be dentigerous. Teeth of the premaxillaries and of the anterior end of the dentary slender conical. Posterior part of dentary and possibly of maxillaries with button-like, flat or only slightly tuberculate teeth.

Vertebræ amphicœlous, neural spines slender. Dorsal ribs single-headed. Coracoid reniform, elongated antero-posteriorly. Scapula narrow. Humerous short, much expanded distally. Radius and ulna about half the length of the humerus; radius with median constriction. Pelvic arch robust, inferior elements not plate-like.

In its fundamental outlines, the skeletal structure in *Thalattosaurus* is strongly suggestive of the *Rhynchocephalia*, but like many of the so-called rhynchocephalian groups it differs so far from the typical forms represented by *Sphenodon*, *Homœosaurus*, etc., that it cannot be included in the same ordinal division. It is likewise so different from all of the other described reptilian families and orders that it must be given an independent position. The family name THALATTOSAURIDÆ and the ordinal name THALATTOSAURIA are therefore used to express its position in the scheme of classification.

Comptes rendus du 6e Congrès international de Zoologie, Session de Berne 1904, pp. 247–248, May 28, 1905.

For the present the *Thalattosauria* may be placed in the superorder *Diaptosauria* of Osborn, though it is doubtful whether it will be retained in that division, or even whether the *Diaptosauria* can hold together when the various forms included in it become better known.

Inside the *Diaptosauria* the closest affinities of the *Thalattosauria* are with the *Protorosauria* and *Rhynchocephalia.* From both groups they differ more widely than these two differ from each other. In many respects, particularly in limb structure, the *Thalattosauria* represent the most highly specialized aquatic forms in the *Diaptosauria.*

Outside of the *Diaptosauria* there are noticeable resemblances to the *Parasuchia* and to the Lacertilians. The common characters are, however, almost without exception, primitive or rhynchocephalian characters which we find persisting in the *Parasuchia* and *Squamata.*

THE TYPES OF LIMB-STRUCTURE IN THE TRIASSIC ICHTHYOSAURIA

INTRODUCTION

OF THE numerous valuable contributions to paleontological literature made by the late Professor George Baur, one of the most interesting was that in which he furnished evidence that the limbs of the Jurassic Ichthyosaurs were highly specialized structures developed in adaptation to aquatic life.[1] In advancing this view he opposed the theory of Gegenbaur and others, who held that they were generalized and intermediate between the pentadactyle limbs of the higher vertebrates and the many-rayed extremities of the selachians. As was shown by Baur, the limbs of the Triassic Ichthyosaurs come nearer to the type of extremity found in the primitive reptilia than do those of the later representatives of the order. The character of the modification of the limbs, and in fact the whole structure of the body in the later Ichthyosaurs, indicated to him that, as a group, they bore the same relation to the Rhynchocephalia that the cetaceans bear to the primitive mammals.

At the time Baur wrote on this subject, the only available Triassic specimens showing the limbs were those from the bituminous shales of Besano in Lombardy. These he separated from *Ichthyosaurus* as a new genus, *Mixosaurus*.

Within the last few years considerable collections obtained from the Triassic of California have brought to light several new groups of Ichthyosaurians differing not a little from the previously known genera of Europe. So many new forms have appeared in this fauna that some of the questions relating to the origin and descent of the Ichthyosauria are reopened. The addition of new material has made the problems more complicated, but it is hoped that before we again reach the limits of profitable discussion it will be possible

American Journal of Science, ser. 4, vol. 19, pp. 23–30, January 1905.

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[1] Ueber den Ursprung der Extremitäten der Ichthyopterygia, Ber. d. xx. Versamml. d. oberrhein. geol. Ver., xx, p. 3.

to add something to our knowledge of the origin and the history of the group.

CHARACTERISTICS OF KNOWN TYPES

At the present time we are acquainted with not less than four types of limbs in the Triassic Ichthyosaurs. One of these is represented in *Mixosaurus*, a second in the genera *Toretocnemus* and *Merriamia*,[2] a third in *Shastasaurus osmonti* and *alexandrae*. The fourth appears in a recently discovered specimen which seems to be specifically identical with *Shastasaurus perrini*. This form evidently represents a genus distinct from the type seen in *S. osmonti* and *alexandrae*, and the name *Delphinosaurus*[3] may be used to distinguish it from the more specialized species.

In *Mixosaurus* (fig. 1) the extremities are of a primitive type. Both manus and pes are pentadactyle,[4] the elements of the limbs are generally quite slender and in many cases have a median constriction. This form is farther characterized by the articulation of the intermedium distally with two or more elements and by the frequent presence of a fourth element (pisiform) on the posterior end of the proximal row in the mesopodial region.

Toretocnemus and *Merriamia* do not differ greatly in limb structure though the vertebrae are of distinct types. In *Merriamia* (fig. 2) the limb has but three digits with the merest vestige of a fourth. There are but three elements in the first row of the mesopodial region and both carpus and tarsus are of a strictly linear type, the intermedium articulating with but a single element distally. In this genus the posterior limbs are much smaller than the anterior. In *Toretocnemus* the posterior limbs equal or exceed the anterior in size and the vestigial fourth digit of the posterior limb appears to have been larger than in *Merriamia*.

The most specialized limb found in the Triassic genera, and one of the most specialized types known in the Ichthyosauria, is seen in *Shastasaurus osmonti* (fig. 4). The anterior limb in this genus is characterized by extreme shortening of all the elements. The

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[2] See G. A. Boulenger, Proc. Zool. Soc. Lon., 1904, vol. i, p. 425. *Leptocheirus* Merriam being preoccupied is replaced by *Merriamia* Boulenger.

[3] *Delphinosaurus* is characterized by much elongated vertebral centra; an unnotched scapula, and the peculiar structure of the limbs described above.

[4] See redescription of *Mixosaurus*, E. Repossi, Atti della soc. ital. d. scien. Natur., vol. xli, fasc. 3, p. 361–372, Tav. viii, ix.

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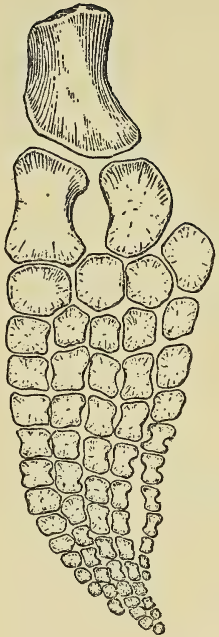

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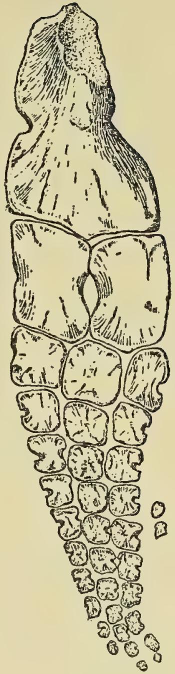

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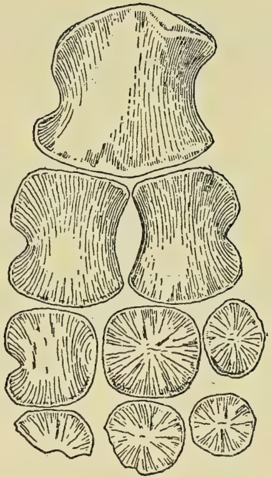

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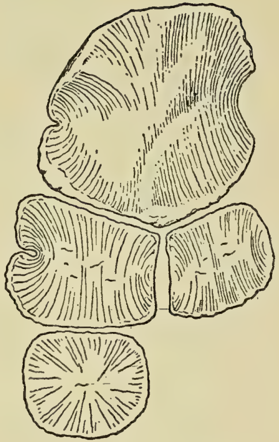

FIG. 1. *Mixosaurus cornalianus.* Left anterior limb. × ½. Slightly modified from Repossi.
FIG. 2. *Merriamia zitteli.* Left anterior limb. × ½.
FIG. 3. *Delphinosaurus perrini.* Left anterior limb. × ½.
FIG. 4. *Shastasaurus osmonti.* Left anterior limb. × ⅙.

humerus is actually as broad as long and is one of the shortest propodial elements known in the reptilia. The epipodial bones are also greatly abbreviated, though separated by a narrow cleft. Of the carpus only the radiale is known. It is as large or larger than the ulna and its margin is entire, while that of the radius shows an anterior notch.

In the recently discovered anterior limb referred to *Delphinosaurus* (*Shastasaurus*) *perrini* (fig. 3) the humerus, radius and ulna are longer than in *S. osmonti*, and the radius and ulna are both deeply constricted. The radiale is narrower and is notched. The carpus is of the linear type and the posterior of the three linear series consists of somewhat smaller bones than are seen in the other two. The elements of the mesopodial and phalangeal regions, as far as known, are rounded and have deeply excavated borders, showing that they lay in heavy pads of cartilage. Judging from the character of the carpus in *Delphinosaurus* and in *Merriamia*, the large radiale in *S. osmonti* indicates that the anterior digit of the manus was relatively larger and the third smaller in *Shastasaurus* than in the other forms. The limb would in that case be reduced almost to a two-fingered type.

Degree of Differentiation

The degree of differentiation shown in the three or four types of limb structure known in the Triassic Ichthyosaurs appears quite remarkable when we compare it with what we find in the Jurassic genera. Three types of limb structure are known from the Jurassic. The most specialized of these is found in *Baptanodon* (fig. 7) and *Ophthalmosaurus* with three very short elements in the epipodial region, five or more digits, and discoidal phalanges. In *Ichthyosaurus*, possessing two short epipodial elements, there are two groups. Of these the Longipinnati (fig. 5) have an essentially linear mesopodial region, a notched radius and usually three to five digits. The Latipinnati (fig. 6) have an alternate arrangement of the mesopodial region caused by the articulation of two or more distal elements on the intermedium; there are generally between five and ten digits; and notches are rarely present on the phalanges, while never on the radius. Compared with these three types the Triassic forms show an unexpected degree of differentiation.

Primitive Characters

In spite of the differentiation shown in the Triassic types, they have all retained certain primitive characters not common in the later forms. All show a separation of the radius and ulna, and in all excepting *Shastasaurus osmonti* these elements are elongated and the radius is constricted or shafted. The presence of these and other primitive characters in so many otherwise different forms furnishes us with much stronger evidence of the origin of the Ichthyosauria from generalized shore forms than could have been given by the single type known to Baur.

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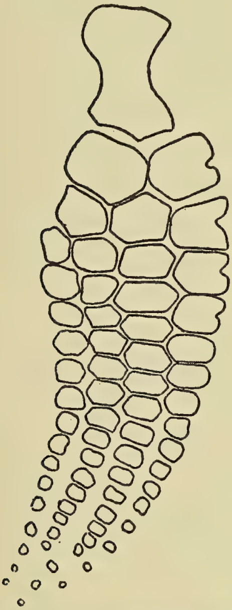

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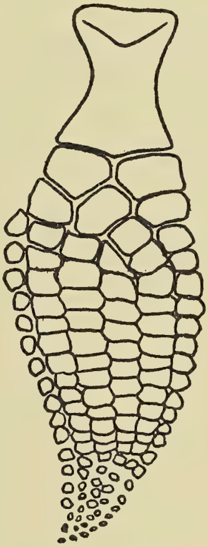

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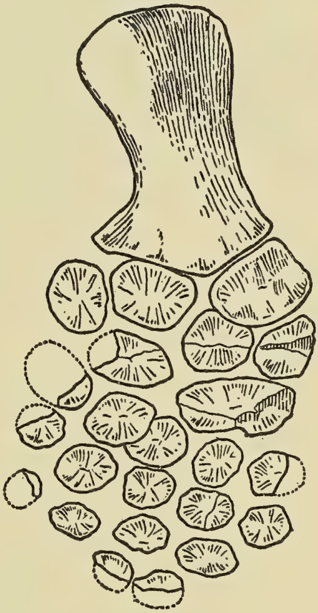

Fig. 5. *Ichthyosaurus quadricissus.* Anterior limb. $\times \frac{3}{8}$. After Fraas.
Fig. 6. *Ichthyosaurus conybeari.* Anterior limb. After Lydekker.
Fig. 7. *Baptanodon marshi.* Anterior limb. After Knight.

Lines of Descent

A comparison of the Jurassic and Triassic genera of Ichthyosaurs with a view to determining the lines of descent shows immediately that no known Jurassic form can be considered as having descended from the specialized *Shastasaurus.* So far as we now know, this group disappeared in the Triassic. *Baptanodon* and *Opthalmosaurus* are also practically excluded from any comparison with the Triassic genera, as they are comparatively late forms and could be derived from the latipinnate Ichthyosaurs as easily as from any of the much older Triassic types.[5]

The views which we hold concerning the descent of the remaining Jurassic groups involve our interpretation of the homologies of the elements in the Ichthyosaurian paddle. On this subject a considerable variety of opinion has been expressed, particularly with reference to the relationships of the mesopodial elements.

Some years ago Lydekker[6] suggested that the most generalized type of limb in the Jurassic Ichthyosaurs is found in the Longipinnati, such as *Ichthyosaurus tenuirostris*. The anterior digit was considered as representing digit II of the primitive limb, digit I having disappeared. Latipinnate forms, such as *I. intermedius*, were supposed to be more specialized, the additional digit in the middle of the hand having been produced by the splitting of digit III. The longipinnate group would then be the more primitive and the latipinnate forms be derived from it by intercalation or splitting of digits.[7]

Strongly suggestive of the latipinnate and longipinnate paddles we find also in the Triassic genera a broad and a narrow type, the broad form occurring in *Mixosaurus*, the narrow form in all of the Californian genera. In the narrow type the limb is even more reduced than in the Longipinnati and is really tridactyle. So far as can be determined, *Toretocnemus* seems to be the most primitive of these forms. The rudimentary fourth digit is larger than in the others and the third digit is as large as the first. In *Delphinosaurus* the third digit is much smaller than the others and in *Shastasaurus osmonti* it was probably smaller than in *Delphinosaurus*. This series showing progressive reduction of the posterior side of the limb indicates that the type is probably not a primitive one, but is derived from an earlier form with five digits.

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[5] Dr. O. P. Hay (Bull. 179 U. S. G. S., p. 463) has, I believe inadvertently, placed the West-American Triassic Ichthyosauria under the Baptonodontidae. Based on this suggestion, Boulenger (loc. cit.) has indicated the descent of *Opthalmosaurus* from *Shastasaurus*. The writer is obliged to regard these groups as probably the most widely separated of all the known Ichthyosauria.

[6] Geol. Mag., 1888, Decade 3, v, p. 310.

[7] Mr. Lydekker has recently expressed himself as in accord with the views concerning the primitive character of the Mixosaurian paddle which are presented in this paper. See p. 136.

While we can understand the origin of the narrow type of paddle in the Trias, the broad form is not so easily explained if we hold that digit number one has disappeared. *Mixosaurus* had five digits of nearly equal size and made up largely of the shafted or primitive type of phalanges. The extremities of this form were, however, *already specialized paddles*, and, if the interpretation of the structure of the paddle of *Ichthyosaurus* given above is correct, we shall have to suppose that in this form digit I was lost and another digit added.

If finger I in *Mixosaurus* corresponds to primitive digit II, the added digit is either below the intermedium or on the posterior border of the limb. The presence of a supernumerary ossicle behind the carpus seems to give support to the idea that the last digit is not primitive, as elements of this character are known to develop secondarily, particularly on the posterior borders of the limbs of aquatic forms. Their presence does not prove the case, however. The supernumerary ossicle may be secondary and the digit primitive, or the presence of the ossicle may be due to upward movement of the last digit along the posterior side of the carpus. Such movements have occurred frequently in Ichthyosaurian paddles, regardless of the theory by which we account for them.

To suppose that one of the digits below the intermedium is of secondary origin would seem almost a violent assumption. That splitting and intercalation of digits have occurred in some of the broad-paddled Ichthyosaurs is beyond question, but evidence of the character which we find in these forms is lacking in the paddle of *Mixosaurus*. The digits are of equal size and their relations to the intermedium are such as one might expect to find in a fairly primitive limb.

Though there is a tendency for the short first digit to disappear in the evolution of a natatory limb, it has not always done so, as for example in the Plesiosaurs. Farther, in the history of the Ichthyosauria two quite distinct types of paddles have appeared; the broad form, illustrated in the Latipinnati and in *Mixosaurus;* and the narrow form, represented in the Longipinnati and in the Californian genera. In all probability the course of evolution has in all cases been fairly direct. That is, the broad paddles have tended toward greater width and the narrow ones toward slenderness. It is not easy to imagine that after limbs had been reduced to a narrow type they would again increase in width. There is therefore good reason to believe that *Mixosaurus* and the Latipinnati have retained the first digit.

If the first digit in the limb of *Mixosaurus* represents digit I of a primitive pentadactyle form, this type may be considered as the most generalized known in the Ichthyosauria. If, on the other hand, the first digit represents number two of the primitive form, the limb can hardly be considered as less specialized than the tridactyle form seen in *Merriamia*, one form having lost two digits, the other having lost one and gained one. Supporting the first suggestion we have the fact that *Mixosaurus* is the oldest described form in which the limb structure is known. The beds in which it occurs are considered by Fraas as the equivalent of some portion of the Middle Triassic, while the Californian genera belong to the Upper Triassic. Evidently *Mixosaurus* is the only described genus which could be considered as ancestral to the Jurassic forms. In the other genera the reduction of the digits has gone farther than in the Jurassic Longipinnati.

It is not impossible that other forms with wider paddles will be found in the American Trias, but up to the present time only the leptochirous or narrow-paddled group seems to be represented. These forms may be closely related to the Longipinnati or may represent a branch of the order which diverged and specialized early. The Longipinnati and Latipinnati may have developed from a persisting primitive stock after the American Triassic forms had become well separated from the rest of the order.

It should be borne in mind that while the evidence furnished by limb structure is some of the most valuable material that we can obtain for use in working out the phylogeny of the Ichthyosaurs, it can hardly furnish the whole foundation for a definite classification. Inside the American group there seems to be considerable variation, though as yet we do not know all of the most important characters of these forms. *Toretocnemus* and *Merriamia* have very similar limbs but differ considerably in the structure of the vertebrae and ribs. It is perhaps a significant fact that of the several genera, *Toretocnemus*, with the largest vestigial fourth digit, appears in its general structure to be nearest to some of the earliest forms of Europe, represented by *Ichthyosaurus* (?) *atavus*[8] from the lower portion of the middle Trias.

University of California, Berkeley

[Baron von Nopsca notified me that *Delphinosaurus* Merriam is preoccupied. Edouard d'Eichwald (1868, Lethaea Rossica ou Paléontologie de la Russie, vol. 2, Période Moyenne, sec. 2, Stuttgart, pp. 1261, 1262) proposed the generic name *Delphinosaurus* for his new species, *Kiprianoffii*.

I therefore take pleasure in proposing to substitute *Perrinosaurus* for *Delphinosaurus* Merriam, 1905, in honor of the late James Perrin Smith.

November 4, 1938 JOHN C. MERRIAM]

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[8] Recent comparisons of *Ichthyosaurus* (?) *atavus* with the types of *Mixosaurus* show that most of the known vertebrae of *atavus* are quite different from those of the true Mixosaurs. So far as is known, they approach most nearly the type of the true Ichthyosaurs. They may belong to *Ichthyosaurus*, possibly to *Toretocnemus*, or may represent an undescribed genus.

A PRIMITIVE ICHTHYOSAURIAN LIMB FROM THE MIDDLE TRIASSIC OF NEVADA

During the last summer an expedition from the University of California spent some weeks in searching for ichthyosaurian remains in the Middle Triassic limestones of Nevada. Both Mr. E. L. Furlong, who directed the work, and Mr. H. M. Evans, who accompanied him, discovered unexpectedly good material, which will make possible considerable advances in our knowledge of these very early forms.

The oldest known Ichthyosaurians of which more than isolated elements or very fragmentary material have been described are the Mixosaurs of the North Italian Triassic. They were obtained from beds which have been held to represent the upper portion of the Middle Triassic. The oldest American Ichthyosaurs of which more than the vertebræ have been described are the Shastasaurs and the accompanying types from the Upper Triassic of California. Up to this time the limbs and arches of the North American Middle Triassic forms have been known only from scattered bones, the description of which has been withheld until more satisfactory material should be obtained.

Among the specimens discovered this year is one which shows the anterior half of the vertebral column, one side of the pectoral arch complete, the first two segments of a pectoral limb, and nearly the entire skull. It was found in the Middle Triassic limestones of Cottonwood Cañon by Mr. H. M. Evans. As nearly as can be determined, these beds seem to be somewhat older than those from which the Mixosaurs of the Italian Trias have been obtained. From the limestone horizon exposed in Cottonwood Cañon two saurian species have been described by Leidy.[1] Both were founded upon portions of vertebrae neither the generic nor specific characters of which have yet been satisfactorily determined. The most common ichthyosaurian species in these beds shows a strong similar-

University of California Publications, *Bulletin of the Department of Geology*, vol. 4, no. 2, pp. 33–38, pl. 5, February 1905.

[1] See Bull. Dept. Geol., Univ. Calif., Vol. 3, No. 4, p. 104.

ity to the imperfect specimens designated as *Cymbospondylus petrinus* by Leidy. The specimen described here is tentatively referred to that species.

The greater number of the Ichthyosaurians showing primitive limb structure which have been described up to this time have been very small forms, and a suggestion of doubt may reasonably have been entertained concerning the probability of large forms from the same beds showing these archaic characters to the same degree. The earlier representatives of most groups are small, and in such forms primitive characters appear frequently when they would not be present in larger members of the same group. It is, therefore, a matter of some significance that the specimen under consideration ranks among the larger Ichthyosaurs, the skull measuring at least a metre in length and the humerus 280 mm. in length.

The elements of the pectoral arch and the limb were found in nearly the position in which they are figured, Pl. 5, excepting the scapula, which had been partly inverted.

The *pectoral arch* differs from that of all ichthyosaurian genera heretofore described. The *coracoid* is sickle-shaped, with a convex anterior border and an acute posterior angle. A foramen of considerable size is situated a little in front of the proximal articulation. This element differs from the coracoid in *Mixosaurus* and in *Shastasaurus* in possessing a convex anterior border, while in both of the other genera the proximal end is narrowed or pedunculate and the anterior border concave in part. Excepting the presence of a distinct perforation, the form is much the same as in the coracoid of the recently described *Delphinosaurus*[2] from the Upper Triassic of California.

The *scapula* is very strongly curved laterally to accommodate itself to the curvature of the body. The anterior and posterior borders are broken somewhat and may have extended out into a hook on each side, as in most of the Triassic forms. The outer border is practically entire and is nearly straight, giving the element somewhat more of the form seen in the true Ichthyosaurs.

The *clavicle* is very large and heavy; much broader and more robust than in *Mixosaurus*. The median end appears to have a large facet for the *interclavicle*, but, strangely enough, that element has never yet been clearly seen in any of the numerous Ichthyosaurians obtained from the West-American Triassic.

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[2] Am. Jour. Sci., Vol. 19, p. 24, Jan., 1905.

Taken as a whole, the pectoral arch resembles that of *Delphinosaurus* more than it does that of any other form. As will appear later, these forms also show evidences of affinity in the structure of the extremities.

As much of the *pectoral limb* as is known shows more resemblance to the type seen in *Mixosaurus* than to any other form. The *humerus* is of much the same type as in *Mixosaurus*, but is if anything a little more slender. Of the two humeri figured by Repossi[3] the principal illustration (fig. 2) represents an extraordinarily long and narrow form. In the other specimen (fig. 1), as in still others, the humerus is almost as broad as it is long.[4]

The epipodial elements are relatively long, as in all of the earlier Ichthyosaurs, and the space between them is very broad. The *radius* is, so far as the writer is aware, the narrowest specimen known in the Ichthyosauria, and the constriction of the median or shaft portion is pronounced. The *ulna* shows the most primitive form known in this group, and at the same time presents certain rather peculiar characters. In all other Ichthyosaurs, excepting *Delphinosaurus*, the posterior border of the ulna is expanded and usually convex. In these two forms it is concave or notched, like the outer or anterior border of the radius; and the median portion of the ulna is drawn in from both sides, showing a true constriction. In *Delphinosaurus* this constriction appears somewhat stronger than in this specimen, but the ulna is much shorter and broader, and the first two segments of the limb are, in general, more specialized.

On both the proximal and distal ends of the ulna the thick, cartilage covered portion of the margin extends far back toward the middle of the posterior side. The thickened margins come so near to each other that the posterior notch is made quite narrow. At the distal end this part reaches around quite to the middle of the shaft, reminding one of the surface against which the pisiform rests in *Mixosaurus*. At the proximal end the surface makes a sharp turn, forming a face which looks as if it might have supported a small supernumerary bone.

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[3] Atti Soc. Ital. Sc. Nat., Vol. 41, Pl. 9, figs. 1 and 2.

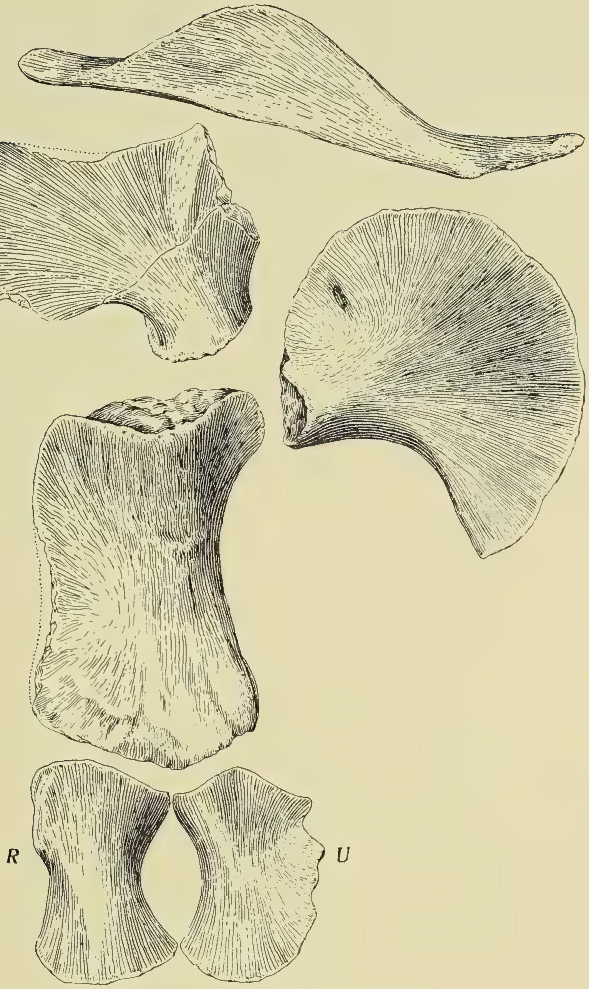
[4] It would appear to the writer that Repossi's figure 4, Plate 9, loc. cit. represents a femur rather than a humerus. It has the form of the femur in other specimens and does not resemble any other described mixosaurian humerus.

With another specimen of the same type as that described above there is an element appearing to represent either a fibula or an ulna showing a very primitive form. The shaft is narrower and the articular surfaces of the two ends are not swung back as far as in the specimen figured here. If this is really an ulna, it represents a stage more primitive than that described above.

Unfortunately, we have no very definite evidence concerning the character of the phalanges in this species. With both this specimen and the one from which the simpler form of ulna was obtained, there are several rounded ossicles resembling carpals. It may be that they are really reduced phalanges which rested in cartilaginous pads as in *Baptanodon*. If this be true, the general primitiveness of the limb would be reduced by some degrees; even in that case, however, the fact that the propodial and epipodial segments of the limb had failed to adapt themselves perfectly, even when the manus had become specialized, would tend only to show more distinctly the influence of an ancestry in which locomotion by crawling or running was more common than by swimming.

As far as we know it, the type of limb found in this specimen is more primitive than any heretofore described. The humerus is hardly more slender than that of certain other Triassic forms, but is among the most slender known, and is not more abbreviated than that of *Mixosaurus*. In the epipodial region, where specialization of a high degree appears in the later members of the order, we find a structure which is somewhat more primitive than any which has previously been observed in the Ichthyosauria. This is a particularly significant fact, when it is noted that the beds in which this specimen was found are probably a little older than those from which we have obtained the most ancient known European specimens showing the limb structure.

University of California
February, 1905



Cymbospondylus petrinus Leidy (?)

Figure one-sixth natural size

Pectoral arch, external side; anterior limb, inferior side. R, radius; U, ulna. The constriction of the ulna is immediately above the letter *U*. The broad, cartilage covered marginal faces of the ulna are discontinued suddenly at the upper and lower ends of the posterior emargination.

THE THALATTOSAURIA

A GROUP OF MARINE REPTILES FROM THE TRIASSIC OF CALIFORNIA

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INTRODUCTION

In the course of the first investigation of the reptilian fauna of the Californian Triassic, the writer examined a peculiar jaw with a differentiated dentition which was exposed on a specimen loaned to him for study by Professor James Perrin Smith. This dentition was seen to resemble the figures of *Mixosaurus* published by E. Fraas,[1] and in a preliminary note on the Ichthyosauria of the Californian Triassic[2] it was referred to that genus. Later preparation revealed the presence of other parts of the skeleton and showed a structure different from that of any Ichthyosaurian. This form was therefore not included among the Ichthyosauria described later from the Californian Triassic.[3]

During the field seasons of 1902 and 1903, expeditions from the University of California carefully worked over the greater portion of the Triassic limestone exposures in Shasta County, and made special efforts to secure material from which a satisfactory determination of the affinities of the unknown form could be made. As the result of this work, a large collection of ichthyosaurian material was brought together and with it a considerable number of specimens representing the new group. The preparation of this material has in all cases been difficult and has necessarily proceeded slowly, but it has resulted in giving us a fair representation of the most important elements of the skeleton.

The acquisition of our knowledge of the Thalattosauria has been made possible through the generous assistance of Miss A. M. Alexander, who has not only contributed the financial support of the field work, and in part also of the preparation of the material for publication, but was herself the discoverer of the specimens which furnish the greater part of our knowledge of the fundamental skeletal structure of the representatives of this group.

Acknowledgments for valuable services in connection with this investigation are also due to all the members of the University of

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[1] E. Fraas, Ichthyosaurier d. Süddeutschen Trias & Jura Ablag., Pl. III, figs. 1–4.

[2] Science, n. ser. v. 15, p. 411.

[3] See Triassic Ichthyopterygia, Bull. Dept. Geol. Univ. Calif. v. 3, no. 4, p. 85, *Dentition.*

California field parties which have worked on the Triassic limestones. To Professor James Perrin Smith I am under obligation for the information which led to the first exploration of the Shasta limestones in search of saurian remains, and for the loan of a valuable type specimen. To Mr. E. L. Furlong I am especially indebted for very efficient assistance extending through every stage of the work, from the collection of the specimens to the final preparation of the material for study. Dr. T. W. Stanton has loaned an important specimen for study and description.

While preparing this report, some weeks were spent in examining typical specimens of forms in related groups. For favors in connection with the study of such material, the writer would express his most sincere thanks to the following gentlemen: Professor S. W. Williston, Dr. A. Smith Woodward, Dr. C. W. Andrews, Dr. E. Fraas, Dr. F. von Huene, Professor E. Koken, Dr. Louis Dollo, Professor Henry F. Osborn, Dr. Lortet.

University of California
March, 1905

Superorder DIAPTOSAURIA

Order THALATTOSAURIA[4]

Marine saurians with abbreviated propodial and epipodial limb segments, elongated facial region, and median external nares. Skull with superior and lateral temporal openings and a pineal foramen. Prevomers and pterygoids as well as jaw elements dentigerous. General structure of skeleton of the rhynchocephalian type.

The group is composed of specialized natatory forms known only from marine deposits. It stands in somewhat the same relation to the typical Rhynchocephalia as that which the Mosasauria bear to the Lacertilia. Evidently derived from a primitive land or shore Diaptosaurian, it has taken somewhat the same course in evolution as was followed later by the Mosasaurs.

Family THALATTOSAURIDAE[5]

Skull elongated, with slender rostrum. External nares separate and not far in front of the orbits. Premaxillaries elongated and forming a large portion of the snout. Premaxillaries, maxillaries and dentaries sculptured on external surface. Superior and lateral temporal openings and pineal opening present.

Prevomers with two rows of heavy, low-crowned teeth. Pterygoids with four or more rows of curved conical teeth. Premaxillaries and anterior end of dentary with slender conical teeth. Posterior part of dentary generally with depressed or flattened teeth.

Vertebrae amphicoelous, neural spines generally high and slender. Dorsal ribs single-headed. Abdominal ribs present. Coracoid reniform, elongated antero-posteriorly. Scapula narrow. Humerus short, expanded distally. Radius and ulna about half the length of the humerus; radius with median constriction; posterior border of ulna convex, radial border concave.

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[4] J. C. Merriam, Bull. Dept. Geol. Univ. Calif. v. 3, no. 21, p. 420.

[5] *Ibid.*

Occurrence and Age

The material upon which the group described in this paper has been based was all obtained in exposures of the Hosselkus Limestone lying between Squaw Creek and Pitt River, in the northern part of Shasta County, California. Specimens were found at numerous localities in the extensive outcrops of this limestone, but the principal collections were made at localities known as Smith's Cove, Bear Cove, Grassy Point and North Fork. The first three localities are all on Brock Mountain, at the southern end of the belt of limestone north of the Pitt. Smith's Cove[6] lies on the southwestern side of the ridge, Grassy Point[7] on the northwestern side, and Bear Cove[8] near the middle of the eastern side. North Fork[9] is a locality on the north fork of Squaw Creek and about two miles northwest of the Kelley Ranch.

The bones occur in practically all horizons of the limestone, but good material is more common, or at least more easily obtained, in the softer, slightly shaly layers well exposed at the localities mentioned.

The limestone section has been divided by Professor James Perrin Smith,[10] on the basis of faunal distribution, into the upper or Spiriferina beds, middle or Juvavites beds, and lower or Trachyceras beds. The softer layers, where the best specimens were obtained, belong in general to the lower or Trachyceras horizon. In the other beds the material seems to be much more fragmentary and little but loose bones or teeth was obtained.

In all cases the remains have been very firmly united with the

[6] Sec. 11 and 12, T. 34 N, R. 2 W, Mt. D. Merid.

[7] Sec. 35, T. 35 N, R. 2 W, Mt. D. Merid.

[8] Sec. 34, T. 35 N, R. 2 W, Mt. D. Merid.

[9] Sec. 1, T. 35 N, and Sec. 36, T. 36 N, R. 2 W, Mt. D. Merid.

[10] See Comparative Stratigraphy of the Marine Trias of Western America, Proc. Calif. Acad. Sci. 3d ser. Geol. v. 1, no. 10, p. 360.

black limestone matrix, and successful preparation was possible only with the aid of an electric engine. As the bones are black, as well as the matrix, it was in many cases impossible to trace their outlines until they had been moistened with hydrochloric acid and allowed to stand for some days. This treatment resulted in the appearance of a delicate blue tint in the bone, evidently due to the presence of the mineral Vivianite, making it possible to follow the lines of contact with little difficulty.

Associated with the thalattosaurian remains are numerous ichthyosaurian bones, a few selachian teeth, occasional ganoid scales, and great numbers of molluscan shells. There are also a few brachiopods, corals and echinoids. The most common of all forms are the cephalopods, which frequently make up a large part of the rock. In the more shaly layers they may be replaced by the lamellibranch genus *Halobia*. A list of the most characteristic genera would include the following: vertebrates,—*Shastasaurus*, *Delphinosaurus*, *Toretocnemus*, *Merriamia*, *Hybodus*; invertebrates,—*Tropites*, *Sagenites*, *Eutomoceras*, *Juvavites*, *Polycyclus Protrachyceras*, *Tirolites*, *Arpadites*, *Arcestes*, *Orthoceras*, *Nautilus*, *Atractites*, *Halobia*, *Rhynchonella*, *Spiriferina*, *Cidaris*.

The invertebrate faunas have been extensively studied by Professor Smith,[11] and are referred by him to the Upper Triassic on the evidence of general striking similarity of the fauna to that of the Alpine Triassic of Europe, even in some cases to the point of identity of species. Also in the case of the Ichthyosauria, almost unquestionable evidence of late Triassic age is given in the stage of evolution or specialization of various parts of the skeleton. In general this is near the stage reached by the Ichthyosauria of the later Triassic of Italy. This is particularly noticeable in the structure of the limbs, girdles and vertebral arches.

The presence of innumerable cephalopods with brachiopods and corals, in a limestone containing for the most part but little argillaceous material, leaves no room for doubt that the deposit was formed in a fairly clear sea, into which there was but little drainage at this point. The reptilian forms which we find in these strata evidently belonged to the typical marine fauna of the late Triassic.

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[11] *Loc. cit.*

Materials Available

The specimen which has furnished the most satisfactory information in this investigation is the type of *Thalattosaurus alexandrae* (No. 9085). Excepting the anterior part of the skull and portions of the limbs and girdles, the skeleton had long been exposed and was largely weathered away. The remaining parts include the anterior two thirds of the skull with a small part of one temporal region. Of the girdles and limbs there are present the scapula, coracoid, humerus, ulna, three bones which represent the lower part of the pelvis and possibly the femur, and some scattered ossicles which may be either carpals or phalanges. Of the vertebral column there are parts of about thirty vertebrae extending in an interrupted series from the head to the anterior caudal region. There are also numerous scattered true ribs and abdominal ribs.

Another specimen (No. 9084), certainly of the same species, shows a portion of the skull with good mandible and quadrate, also both humeri, a radius and several well preserved dorsal vertebrae.

Two other smaller skulls having the same size and form are also referred to *Thalattosaurus* but probably do not belong to the type species. One of them (*T. shastensis*, No. 9120) shows the inner side of the posterior half of a skull in good state of preservation. With it are several good vertebrae, limb bones, ribs, abdominal ribs and teeth. In the second specimen the posterior three fourths of the skull are present, fairly preserved but very difficult of preparation.

A fourth skull, the type of *T. perrini*, shows the greater part of the mandible, maxillary and palatine, with portions of numerous other elements of the skull.

The type of the genus *Nectosaurus* consists of the posterior two thirds of a mandible with the frontals, parietals, a prefrontal, a postfronto-orbital and part of a quadrate. Several loose jaws, portions of skulls, vertebrae, ribs, etc. are also referred to this genus.

General Skeletal Structure

Skull

Plates I–VI

Considerable parts of the head are shown in five specimens. In all of this material, excepting the type of *Thalattosaurus*, the skulls are small and the bones thin and difficult to prepare.

The skull in the type specimen was fortunately broken into four segments by wide vein-filled cracks. In preparation, these segments were separated so as to show all sides of the bones and the cross-sections of the skull. The sections have been of especial value, serving as checks in observations on the position and arrangement of the bones.

The restorations of the skull (Text figs. 1 and 2, and Pl. VI) were based on the type specimen. The temporal and fronto-parietal regions and a portion of the mandible are restored from *T. shastensis*.

Facial Region.—As is shown in Plate I, the facial region of this skull is very slender. The snout was narrow, exhibiting some resemblance to that of the long-headed Mosasaurs.

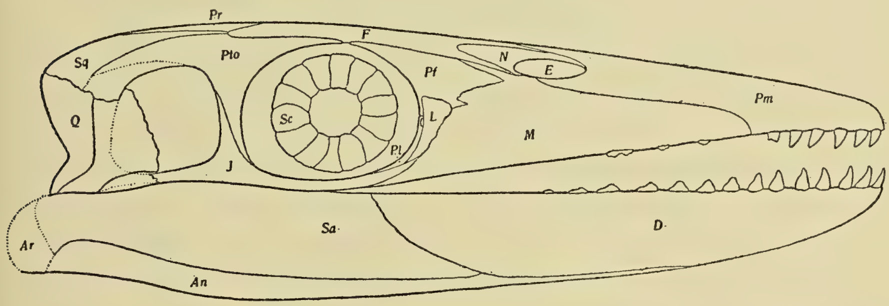

FIG. 1. *Thalattosaurus alexandrae.* Reconstructed skull, lateral view, × $\frac{8}{25}$. Pm, premaxillary; *M*, maxillary; *N*, nasal; *E*, superior nares; *F*, frontal; *Pr*, parietal; *Pf*, prefrontal; *Pto*, post-fronto-orbital; *J*, jugal; *L*, lachrymal; *Pl*, palatine; *Sc*, sclerotic ring; *Sq*, squamosal; *Q*, quadrate; *Ar*, articular; *Sa*, supra-angular; *An*, angular; *D*, dentary.

Over a large part of the external surface of both maxillaries and premaxillaries, the rostral region has *sculptured* into it a series of pits and grooves. They run longitudinally on the premaxillaries but have in general a radial arrangement on the maxillaries. They appear also on the anterior portion of the lower jaw. While not so strongly impressed as in the Crocodilia or Stegocephalia they are nevertheless a characteristic feature of the skull in this group.

The *superior narial openings* were situated only a short distance in front of the orbits and are almost immediately above the inferior openings. They are separated by a heavy bar consisting of the nasals, frontals and premaxillaries. The superior openings are bounded on the external side by the nasals, the premaxillaries and apparently to a slight extent by the maxillaries. Anteriorly they are closed by the premaxillaries. In the type of *Thalattosaurus* there are also present certain peculiar elements which have somewhat the appearance of anterior prolongations of the prefrontals rising along the anterior margins of the openings. The character of these elements is, however, somewhat doubtful.

The greater portion of the snout is formed by the *premaxillaries*, which extend back to form part of the boundaries of the narial openings. The needle-like posterior ends reach back of the nasals and are thrust between the median anterior prolongations of the frontals. In the cross-sections (Pl. II, figs. 1*a*, 1*b* and 1*c*) the premaxillaries are seen to be distinctly separated. At section *c* (Pl. II, fig. 1*c*) each element shows two large dependent branches, one of which forms the external lateral wall of the snout, the other resting between upward prolongations of the prevomers. The alveolar margin is set with conical, slightly recurved teeth. The extreme anterior end of the premaxillary is not known, but judging from the extent to which this bone has narrowed anteriorly, as also from the character of the nearly perfect termination of the lower jaw, only a very small fragment is missing from the type specimen. The dentigerous portion of the premaxillary seems almost to have equaled that of the maxillary in length, though the inferior margin of the maxillary is longer.

In *T. alexandrae* the posterior end of the *maxillary* is considerably expanded vertically, reaching upward to the lateral prong of the frontal, with which it is folded into the prefrontal (Sec. *a*, Pl. I, fig. 1 and Pl. II, fig. 1*a*). The posterior part of the alveolar margin is not well preserved and it is not known whether it bore teeth. No part of this border appears to be pitted or grooved for the reception of teeth. On the anterior portion there are two prominences which seem to represent fangs from which the crowns have been almost entirely removed.

In *T. perrini* the maxillary dentition is very well shown excepting on the posterior portion of the jaw, which seems to have been edentulous. The teeth are sharply conical and are set in deep, distinct pits.

The *nasals* are clearly shown in the type of *Thalattosaurus*. They are not large and border mainly the median and posterior sides of the superior nares. They do not meet medially but are separated by the frontals and premaxillaries. The posterior ends rest between the forks of the frontals. A tendency toward separation of the nasals by extension of the frontals and premaxillaries is seen in many reptilian skulls, particularly in rhynchocephalian, lacertilian and sauropterygian forms, but such complete separation as is shown here is so rare that it may be considered an important character. The nearest approach to this structure is seen in the Sauropterygia.

In that group the nares are situated close to the orbits and are either median or subterminal. In all cases the premaxillaries form a large share of the snout. In the Nothosaurs the nasals have almost the same form as in *Thalattosaurus*, and the premaxillaries are thrust back between the nares though not in contact with the frontals. In *Pistosaurus* the premaxillaries touch the frontals, separating the nares and the small nasals. In *Plesiosaurus* the premaxillaries are in broad contact with the frontals. In *Dolichorhynchops*, recently described by Williston, the premaxillaries extend back to the parietals, separating even the frontals.

Fronto-parietal Region.—This region is particularly well shown in the specimen of *Thalattosaurus* represented in Plate III. Both frontals and parietals are distinctly paired and on both the superior surface is nearly smooth, being marked only by fine lines and pits. The *frontals* are relatively large. Their postero-external angles reach far back and partly clasp the anterior ends of the parietals. The anterior ends are deeply incised for the reception of the nasals. The median anterior forks extend forward as far as the middle of the superior nares, while the lateral forks reach almost if not quite to the outer border of the nares.

The *parietals* are much smaller than the frontals and are also separated by a median suture. A large parietal foramen lies between the two elements, but is a considerable distance behind the coronal suture. The posterior outer angles of the parietals are produced backward around the outer side of the superior temporal openings for more than half the length of the upper temporal arch.

In figure 2*a*, Plate IV, what appears to be the *squamosal* is seen to reach forward over the post-fronto-orbital to touch the frontal. If this is the normal relation of these elements, the outer border of the parietal is separated from the post-fronto-orbital. The median portion of the parietal is also produced backward as a slender arm and was probably in contact with the squamosal. The two posterior arms seem almost to have surrounded the upper temporal opening, giving to the skull an altogether peculiar character in this region.

Temporal Region.—The skulls appear to be characterized by the presence of both superior and lateral temporal openings. The *superior openings* are considerably smaller than the lateral. Judging from the specimen seen in Plate III, the posterior ends of the parietals were very slender and were dropped some distance below the level of the roof of the skull, so that the superior openings faced backward somewhat, as in *Belodon.* The anterior half or two thirds of this opening was enclosed by the parietal. The posterior boundaries have not been seen. They were probably formed by connection of the parietal and squamosal, though the supraoccipital may have intervened as seems to have been the case in *Sauranodon.*

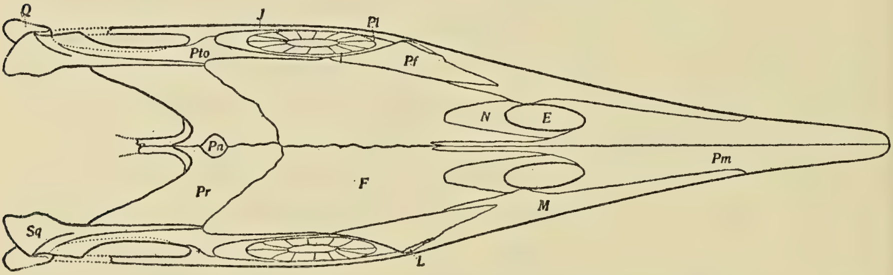

FIG. 2. *Thalattosaurus alexandrae.* Reconstructed skull, superior view, × ⅓. *Pm,* premaxillary; *M,* maxillary; *N,* nasal; *E,* superior nares; *F,* frontal; *Pr,* parietal; *Pn,* pineal foramen; *Pf,* prefrontal; *Pto,* post-fronto-orbital; *J,* jugal; *L,* lachrymal; *Pl,* palatine; *Sq,* squamosal; *Q,* quadrate.

The relatively large *lateral temporal openings* are seen in two specimens (Pl. III, fig. 2, and Pl. IV, fig. 2*a*). The boundaries are not perfect, even in the more nearly complete specimens, owing to the absence of the quadratojugal. In both instances, however, the jugal sends backward a long and strong process extending more than half the distance to the quadrate, and in one specimen the posterior end of this process is roughened as if from contact with a quadratojugal. Under these circumstances it would be difficult to believe that the *inferior bar* was incomplete. Should we assume that it was not complete it would be necessary to suppose that it is caught, as it were, in the process of breaking down, as no form losing the lower bar retains a posterior jugal process similar to that shown here. In reality there is hardly reason for supposing that the lower bar was even weak, as the posterior process sent out from the jugal is not stronger than it is here in many forms in which this arch is considered well developed.

The *upper temporal bar* is certainly made up to a great extent of the large post-fronto-orbital and the squamosal, as seen in Plate IV, figure 2*a*, with the addition of the outer posterior process of the parietal lying on the median side of the bar. Even on the most complete specimens (Pls. III and IV) it has been impossible to determine certainly whether a prosquamosal is present or not, as the character of the bone is such that the sutures immediately above the quadrate are very difficult to determine. On what is taken to be the quadrate in a fragment of the temporal region of the type of *Thalattosaurus* (Pl. II, fig. 4) there rests a downwardly projecting arm which appears to be a part of an element that belonged to the lower side of the upper temporal bar. Evidently it extended down the outer wing of the quadrate, almost if not quite to the quadratojugal. The inner side of this bone, as also of that resting on the summit of the quadrate, is weathered away and it is not impossible that they were originally connected. If united, the squamosal must have had a form somewhat similar to that of *Sphenodon*. If separated, the lower element is apparently a discrete prosquamosal.

Quadrate, Suspensorium.—The *quadrate* is well shown in position in one specimen (Pl. III, fig. 2) and macerated out, though associated with the posterior end of the mandible and the cranium, in another (Pl. II, figs. 2*a* and 2*b*). It is of distinctly rhynchocephalian type, though approaching the lacertilian form in the development of a stronger posterior hook and a broad exterior wing. While the posterior side of the distal end is rounded upward the anterior side is distinctly flattened as if from contact with a quadratojugal. The presence of a high extero-lateral wing seems to preclude the possibility of there having been a fenestra between the quadrate and quadratojugal, as in the typical Rhynchocephalia, though there may have been a small opening near the distal end.

The relation of the quadrate to the temporal bones is such that it must have been immovable, in contrast to the general relations in the Squamata.

Orbital Region.—The specimens of *Thalattosaurus* show portions of large *sclerotic plates* in the orbits. They are similar in form to those seen in the Mosasaurs. In at least one instance a plate is deeply grooved on the margin, as occurs in forms in which the sclerotic ring is particularly heavy and strong.

In the boundaries of the upper side of the orbit the prefrontal and post-fronto-orbital come so close together that the frontal hardly appears on the rim of the orbit. The posterior boundary is formed by the heavy ascending process of the *jugal*, and a single upper element evidently representing both the post-frontal and the post-orbital. No evidence has been obtained which would tend to indicate the existence of a separate postfrontal resting above this bone. The apparent contact of the squamosal with the frontal might be interpreted to mean that a greatly reduced postfrontal is fused with the anterior arm of the squamosal, but until we have more definite proof of this it can be considered only as a mere possibility.

The *prefrontals* are large robust elements extending from the middle of the upper boundary of the orbit forward along the inner side of the maxillary.

The small *lachrymal*, extending over only a limited area of the face, is well shown in the type of *Thalattosaurus* (Pl. I, fig. 1, *L*). The lachrymal foramen is also distinctly seen here. In cross-section *b*, Plate II, figure 1*b*, *A* there is seen a peculiar element apparently distinct from the nasals, maxillaries, premaxillaries and prevomer. If such is really the case, this is probably an anterior prolongation of the prefrontal. This would, however, require an extraordinary enlargement of the anterior end of this bone, and further evidence is required before its relations can be satisfactorily determined.

Palatine Region.—It is in the palatine region that some of the most distinctive characters are seen in the members of this group. The general aspect here is of a primitive form in which the rostral region, and in it particularly the vomerine dentition, exhibits distinctive specialization.

The position and relations of the *prevomer* are best shown in the type of *Thalattosaurus* (Pl. I, fig. 2, and Pl. II, figs. 1*b* and 1*c*). It is here seen to lie largely between the maxillaries although reaching far forward along the rostrum. It is much elongated antero-posteriorly and has in general a sphenoidal form. So far as can be determined from the sections no median suture is present, though the structure may have been paired. From the median portion of the posterior end three laminae project backward, the median plate being much smaller than the others. On either side of these laminae the posterior margin shows a regularly rounded excavation, representing the anterior borders of the inferior nasal openings. The posterior plates evidently connected the prevomer with the palatines or the pterygoids. The palatal surface of the prevomer bears two long rows of teeth following the lateral margins. Posteriorly they are separated by quite a distance, but they approach each other near the middle of the bone and run parallel from that point forward.

In another specimen (Pl. v, figs. 2*a* and 2*b*), which was found separated from other skeletal remains, exactly the same form is shown. In the type of *T. perrini* (Pl. v, fig. 3) a part of a prevomer of the same general form is known. Fragments of several other specimens have been found to show corresponding structure. On all the specimens in which the anterior end of the prevomer is shown, the dentigerous portion of the bone is seen to bend downward sharply in the middle. In the specimen which was entirely separated from other bones of the cranium (Pl. v, figs. 2*a* and 2*b*), the drop is very pronounced and cannot be fully accounted for by distortion. A similar but less prominent bend is seen in the prevomer of *T. perrini*. Evidently the middle portion of the prevomer was produced downward somewhat, making the tooth row convex. The downward sweep is, however, very pronounced and must have carried the vomerine teeth down to meet the low posterior teeth of the mandibular series.

The form of the prevomer seen here suggests the Rhynchocephalia, but differs from the known types in the character of the dentition. The broadened teeth of the posterior portion of the bone had possibly a function somewhat similar to that of the smaller vomerine teeth of the Choristodera; but they were much less numerous, were much larger, and were confined to the lateral margins of the palatal surface.

The *inferior narial* openings in *Thalattosaurus* are large and are situated almost immediately below the superior openings, the anterior borders being slightly anterior to the posterior borders of the upper openings. The external borders are formed in part by the maxillaries, as the anterior ends of the palatines do not appear to come in contact with the prevomer here in the manner in which they do in the Choristodera.

The anterior ends of the *palatines* are turned upward behind the narial openings and are deeply grooved to form the posterior walls of the nasal passages. As seen in section *a* (Pl. II, fig. 1*a*) the external border of the palatine is enfolded by the thin posterior end of the maxillary. In *T. perrini* (Pl. IV, fig. 3) the same relations are seen, only the narial opening is smaller. The median border of the palatine swings far around the nares here as if it had probably joined the prevomer broadly. The relations of the posterior and median sides of the palatine are only imperfectly known. The groove on the median side of the element (Pl. IV, fig. 3) is not such a contact as would occur if the corresponding element from the other side were met here. The presumption is that the anterior end of the pterygoid passing along the median border of the palatine was in contact with this surface.

In none of the skulls examined have there been found any indications of the existence of teeth on the palatine. In two specimens (Pl. III, fig. 3 and Pl. IV, fig. 3) this element can be seen in place and has been followed backward for a considerable distance without showing any traces of teeth, though they are well shown on other elements. The teeth shown close to the palatine on Plate IV, figure 3, are entirely distinct from it. They probably belonged to the pterygoid.

One of the most remarkable features of the type specimen of *Thalattosaurus* is a peculiar dentigerous bone which lay below the palatine region and above the separated rami of the mandible. Considering the position of the specimen, the character of the material, and the fact that no bones of other animals have been found in the matrix, there can be no reasonable doubt that it belongs to this skull. This bone (Pl. V, figs. 1*a*, 1*b* and 1*c*) is held to be the *pterygoid*. It consists of a narrow, thick plate, one border of which bore five rows of teeth. The opposite margin of the plate supports a high, thin, triangular wing standing almost parallel with the tooth-bearing surface. The surface of this wing is marked on one side by radiating sculpture somewhat like that of the maxillary, excepting that it is largely in relief. The acute end of the wing is drawn out to a very thin edge. The broad end is considerably thicker and shows a deep groove where it was probably in contact with the quadrate.

The *pterygoid teeth* are in four rows with alveoli for a fifth. Unfortunately the crowns of nearly all were broken or weathered off and only the well preserved fangs remain. The teeth are all set in distinct pits and are inclined sharply toward the thickened end of the bone.

Considering that the palatine is edentulous and the vomerine teeth have specialized toward the low, broad type present only in a single row on each side, it is rather remarkable that the pterygoid teeth should be so numerous and evidently of the recurved, conical type. There is, however, no apparent escape from the conclusion that such is the case. Apparently the vomerine teeth served largely as crushers, while the pterygoid teeth assisted deglutition. The type of pterygoid represented here does not correspond exactly to any that has so far come to the writer's notice, but is not far removed from the type seen in some Rhynchocephalians.

In one specimen of *T. shastensis* (Pl. III, fig. 2, *Ep*) there appears to be a fragment of an *epipterygoid* in its natural position above the pterygoid. No ectopterygoid has been recognized.

Mandible.—(Pls. I, III and IV). Though no single specimen shows the whole of the lower jaw, overlapping portions of several exhibit the whole structure of both the inner and outer sides. The jaw is characterized by the sculpturing of the dentary, as shown in the type of *Thalattosaurus*, by the length of the angular, and by the prominence of the coronoid process.

The *dentary* does not appear to form the lower border of the outer side of the jaw excepting along the most anterior portion, owing to the extreme forward extension of the angular. The connection of the rami at the symphysis was loose and they have fallen away from each other in all of the specimens examined.

In *Thalattosaurus* the teeth upon the dentary extend back almost to the extreme posterior end of that bone, where they are low down on the inner side of the jaw. They are either set in depressions or appear to be fused to the jaw.

The extreme posterior end of the jaw is formed by the *articular*, which extends forward to be covered anteriorly by the splenial. The supra-angular is large and makes up the greater part of the posterior half of the jaw. The *angular* also forms a considerable part of the outer side of the jaw and ranges forward well toward the anterior end of the ramus. A large *splenial* covers a considerable part of the inner side of the jaw. It extends back to a point below the middle of the coronoid and may reach forward almost, if not quite, to the symphysis.

The most characteristic feature of the mandible is the form of the *coronoid*. This element is broadly expanded over the inner side of the ramus and reaches with its upper border high above the supra-angular as a coronoid projection. The form of the coronoid is strongly suggestive of the Lacertilia, though it is approached in the true Rhynchocephalia. Particularly is this noticeable in the jaw of *Nectosaurus*, which taken by itself would appear unquestionably lacertilian.

Dentition

The dentition is well shown in the type specimens of *Thalattosaurus*, as also in the lower jaw of the type of *Nectosaurus*, and more or less imperfectly in most of the other specimens. In addition to the jaw elements, the pterygoid and prevomer are dentigerous while the palatines are not known to have carried teeth.

Teeth of the Jaws.—The *insertion* of the teeth on the upper and lower jaws varies considerably within the group. In *Thalattosaurus* the teeth of both upper and lower jaws seem to rest in pits, which may be in elevated bases formed by the alveolar margin. In some cases they appear to be fused with the jaw bone. In *T. perrini* the teeth of both jaws rest in distinct pits. The depth of the pit and the general character of the insertion are to a considerable extent dependent on the form of the crown. The slender conical, anterior teeth are very deeply set in the jaws, while the pits for the low, broad-crowned, posterior mandibular teeth are much shallower. This may have been the case in *T. alexandrae* also, but the preservation of the anterior portion of the jaw of the type specimen has not permitted a satisfactory investigation of the insertion.

One of the diagnostic features of *Thalattosaurus* is found in the remarkable *differentiation* of the mandibular dentition. In *T. alexandrae* (Pl. 1, fig. 3) the crowns of the anterior teeth are slender conical with a slight lateral compression, while the most posterior teeth are very broad and nearly flat-crowned, resembling considerably the form of the teeth of *Placodus*, although very much smaller.

The teeth in the middle portion of the jaw grade from the flat form to slender conical, through the gradual development of a tubercle on the antero-external portion of the crown. This elevation increases in size until it comprises the whole crown. Unfortunately the dentition of the upper jaws is not well known except on the anterior portion, where the crowns are conical as on the opposing portion of the mandible. Upon the maxillary, portions of two or three fangs are seen, but the crowns have been destroyed.

In *T. perrini* (Pl. IV, fig. 3) the dentition of the lower jaw shows again the conical anterior teeth with laterally compressed, low-crowned posterior teeth. The depression in the latter is, however, very much less than in *T. alexandrae*. In the upper jaw all of the teeth are conical. There do not appear to be any low-crowned or laterally compressed maxillary teeth. The most posterior portion of the maxillary was apparently edentulous and it is evident that the posterior vomerine teeth were in contact with the posterior portion of the mandibular dentition.

In the type of *Thalattosaurus* the perfectly preserved tip of the crown of an anterior mandibular tooth shows very faint wrinkles in the enamel. On the depressed posterior teeth the wrinkling of the enamel is more pronounced and in some instances a faint tuberculation is visible. A single loose tooth found with the jaws of this specimen has an elongated, somewhat compressed crown covered with numerous strong longitudinal striae.

Associated with the head bones of *T. shastensis* are several loose teeth showing the form very distinctly. In all of these the crowns are conical, but they vary considerably in length and thickness. The slender, curved teeth (Pl. IV, fig. 2*b*) are probably from the anterior portion of the jaws, and the shorter, heavier ones (Pl. IV, fig. 2*c*) from the middle region. The crowns are all supported on heavy fangs, such as are present in teeth inserted in pits. The enamel is marked with numerous fine, longitudinal wrinkles or striae somewhat finer than those on the corresponding teeth of *T. alexandrae*.

In no case has any evidence been obtained which would tend to show that the bases of the teeth have a folded internal structure as in the Ichthyosauria and Choristodera.

Vomerine Teeth.—In all specimens, so far as is known, vomerine teeth are present in only two rows, which are set upon the outer edges of the prevomer instead of next the median line. The rows converge anteriorly and near the middle of the prevomer they are very close together. From this point forward they run approximately parallel. In the posterior, diverging portions of the rows the crowns are very low and roughly triangular in cross-section. In the parallel portions the crowns are slightly higher. A very striking feature of the vomerine dentition is the downward sweep which it takes, the lowest point of the curve being at the place of convergence of the tooth rows. The teeth in this region seem to have come in contact with the low-crowned teeth near the middle of the lower jaw. The posterior vomerine teeth evidently met the posterior teeth of the mandible.

The vomerine teeth are set in depressions and where seen in a cross-section of the prevomer (Pl. II, fig. 1*c*) they are known to extend a considerable distance into the bone. The enamel is ornamented with a large number of fine wrinkles radiating from the apex of the crown.

Pterygoid Dentition.—Closely set teeth were present in at least five rows on the heavy median plate of the pterygoid. They are of slender conical form and each is set in a distinct pit of considerable depth. Unfortunately the crowns have not been well preserved. They are all nearly circular in cross-section and the enamel seems to have been slightly wrinkled toward the base.

Function.—The dentition of the Thalattosaurs is evidently that of swiftly swimming forms feeding in a large measure upon fish. The character of the posterior mandibular and vomerine teeth of *Thalattosaurus*, indicating a crushing function, probably means that this type fed also in part upon some creature with a shell which could be easily crushed. Such forms would have been found in the numberless cephalopods of this epoch, and they doubtless furnished a portion of the food of the Thalattosaurs.

Vertebrae

PLATE VII, FIGS. 1–5

In the type specimen of *Thalattosaurus alexandrae* parts of over thirty vertebrae are shown. They represent the cervical, dorsal and anterior caudal regions. A number of loose vertebrae in a fair state of preservation are associated with other specimens.

In *Thalattosaurus* the centra of the *anterior dorsals* (Pl. VII, figs. 1 and 2) are nearly circular in vertical, transverse cross-section. The anterior and posterior faces are concave but not so deeply excavated as in the Ichthyosauria, the wall between the two faces representing more than half of the antero-posterior diameter of the centrum. The upper arches are rather slender and are not greatly thickened. The anterior margins are sharp. The posterior edges seem to be blunted or rounded. Strong zygapophyses are present. A characteristic feature of these vertebrae seems to be found in the closer attachment of the upper arches to the centra than we find in the Ichthyosauria. In this respect they resemble the vertebrae of the Plesiosaurs and Crocodiles.

An upper arch of *T. shastensis* (Pl. VII, fig. 4) shows the structure of the neurocentra better than in any other specimen. The spine is wider antero-posteriorly and is not so high as in *T. alexandrae*. Possibly this is due in this case to the arch having occupied a more anterior position than the arch of *alexandrae* figured (Pl. VII, fig. 1). The zygapophyses are large and strong and the facets well separated.

The ribs of *Thalattosaurus* articulate on a single wide apophysis, the upper portion (diapophysial) of which is situated above the middle of the centrum. The surface of articulation is considerably narrowed in the middle but the apophysis is not seen to divide into distinct di- and par-apophyses. In the dorsal vertebrae examined, the uppermost portion of the rib head has been in articulation with the base of the neural arch.

In the *caudals* of *Thalattosaurus* (Pl. VII, fig. 3) the centra are somewhat angular in cross-section, though not greatly flattened laterally. The upper arches are very slender and relatively thick. Large and prominent zygapophyses are present. The faces are sharply separated and almost vertical in position. A slight elevation of the neural spines may indicate a little broadening of the tail. The structure of the vertebrae seems to indicate that the tail of *Thalattosaurus* was not a highly specialized sculling organ as in the Ichthyosauria and the Thalattosuchia. The propelling function may have been performed largely by the limbs as in the Plesiosauria. Evidence pointing in this direction is furnished by the bones of the pelvic arch, which are relatively large and robust for a swimming animal of this size.

Ribs

PLATE VII, FIGS. 6 AND 7

True Ribs.—Many fragments of ribs are present in the type specimen. In these the shaft is apparently about as heavy as in the Ichthyosaurs. The middle of the shaft is grooved on one side, the distal end is round in cross-section. In the single specimen in which the head is preserved but one articular surface is seen. In a specimen of *T. shastensis* showing several rib fragments associated with the bones of the head and the pectoral arch (Pl. VII, fig. 7) the shaft is rather heavy, is grooved anteriorly, and there is a single wide articular face as in *Shastasaurus.*

In the dorsal region the rib heads have articulated largely on the broad apophyses on the centra of the vertebra, but the uppermost portion rested also in part against the base of the upper arch.

Abdominal Ribs.—On one specimen (No. 9120) numerous abdominal ribs are present. They are long, and compared with the dorsal ribs are exceedingly delicate and slender. It has not been possible to distinguish between median and lateral pieces.

In the type specimen the lower portion of the skeleton with the abdominal ribs had been largely destroyed, but a single fragment apparently representing an abdominal rib is seen between the distal ends of the dorsal ribs.

Limbs and Girdles

PLATE VII, FIGS. 8, 9 AND 10; PLATE VIII

The pectoral and pelvic arches are both represented in the type specimen of *Thalattosaurus.* Apparently neither arch has been moved very far from its original position with reference to the remainder of the skeleton.

Pelvic Arch and Posterior Limb.—In the pelvic region of the type specimen there are parts of several bones evidently representing a portion of the pelvis and probably some of the elements of a hind limb. Only two of these bones are complete enough to permit identification. Corresponding to one of them there are in the collections two much better specimens (Pl. VII, figs. 8 and 10) giving a fair idea of its form. This element is larger than the other and differs from it somewhat in form. It exhibits characters which are not particularly definite and might permit its identification as either of the inferior elements of the pelvic arch or possibly as the femur. It is narrowed somewhat below the proximal end or head and is considerably broadened distally. The expanded anterior margin of the distal end is thin and slightly decurved. The distal portion is thickened, excepting in the middle of the end, and is excavated along the distal border. The proximal end is also excavated. On the more strongly concave side of the neck there is a small foramen in all three specimens.

This element shows some resemblance to a femur, and when first examined was thought to represent that element. It also resembles the pubis in the form of both ends, in the curvature of the shaft, and in the twist of the outer margin. The small foramen near the proximal end might occur behind a trochanteric elevation of a femur or in the pubis. If this is the femur it represents a type of extremity quite different from that seen in the anterior limb, the distal end being turned sharply backward and slightly upward. Propodial elements of this kind are not uncommon in natatory reptiles, but when present in the hind limb, the forelimb is usually, though not always, of a similar character.

The other element belonging in this region (Pl. vii, fig. 9) is again of somewhat indefinite form. It is quite similar to the first mentioned element but is smaller and shows a greater expansion of the median portion, producing a prominent wing. This bone might be either pubis or ischium but is probably the latter.

A fragment of another large element lying next the ischium may represent the ilium or the femur. It is nearly straight and appears to be almost circular in cross-section.

However we may interpret the elements which have been discussed, it is evident that at least one of them must belong in the inferior portion of the pelvis, and that the characters of either or both of them are such as to show that the pelvis was not of the plate-like form usually seen in the primitive Diaptosauria.

Both of the elements described from the pelvic region of the type specimen are large compared with the coracoid, scapula and humerus. No matter how we interpret them, they show that the posterior limbs were possibly more powerful than the anterior, reminding us of the peculiarly specialized Thalattosuchia of Fraas.

Pectoral Arch.—The pectoral girdle is represented by the coracoid and scapula. No clavicle or interclavicle has as yet been discovered. Several fragments of large bones associated with the pectoral girdle may represent one or both of these elements. The *coracoid* (Pl. VIII, fig. 1) is reniform and has somewhat the form of the coracoid in the ichthyosaurian genus *Merriamia* from the same horizon. It is, however, more distinctly reniform, having a sharply concave exterior margin.

The *scapula* (Pl. VIII, figs. 2 and 3) is comparatively narrow resembling that of the Crocodilians, Parasuchians, the later Ichthyosaurs, and most of the rhynchocephalian forms. It differs from that of the Triassic Ichthyosaurs in lacking the considerable distal expansion.

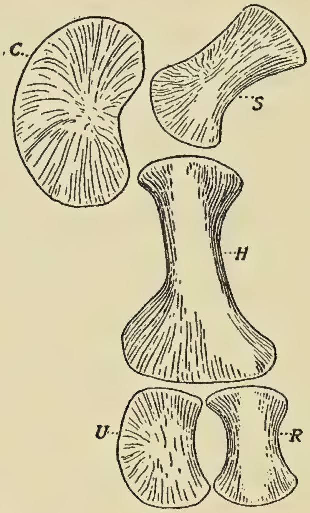

FIG. 3. *Thalattosaurus alexandrae.* A portion of the right pectoral arch and limb seen from above, × $\frac{3}{8}$. *C*, coracoid; *S*, scapula; *H*, humerus; *R*, radius; *U*, ulna.

The structure of the pectoral arch, so far as known, seems more primitive than that of the Triassic Ichthyosaurs and is of distinctly rhynchocephalian type.

Anterior Limb.—Elements belonging to the anterior limbs are found in the type and in two other specimens. In the type the humerus and the ulna are present. In another specimen both the humeri are well preserved and with them is a nearly perfect radius.

The *humerus* (Pl. VIII, figs. 4*a* and 4*b*) is considerably expanded dorsoventrally at the proximal end through the development of a very heavy pectoral ridge extending to the middle of the shaft. The distal end is greatly broadened, its width equaling two thirds the length of the bone. In either inferior or superior view the middle of the shaft appears more slender than is actually the case, owing to the fact that the expanded ends are twisted at right angles to each other. Both the proximal and distal ends seem to be deeply excavated, and evidently supported large cartilaginous caps. In one specimen (Pl. VIII, fig. 4*b*) a small foramen is seen near the distal end of the pectoral ridge. Although it is quite small it probably represents an epicondylar foramen.

The humerus of *T. shastensis* (Pl. VIII, fig. 8) is perhaps a little more slender than in *T. alexandrae*, but is imperfectly represented in the figures, as it is considerably weathered.

The *radius* (Pl. VIII, fig. 5) is shafted, but shows considerable distal and proximal expansion. Its length is about one half that of the humerus. The *ulna* (Pl. VIII, figs. 6 and 7) is convex posteriorly and concave anteriorly, showing no median constriction.

Several rounded ossicles resembling the phalanges of *Baptanodon* have been found associated with the limb and arch bones of the type specimen. Undoubtedly they represent carpals or phalanges, and there is a possibility that some at least are phalangeal elements.

The *type of limb* represented in this form is that of an aquatic animal, as is shown particularly in the extreme shortening and broadening of the humerus and of the epipodial bones. Such indications as are given in the possible character of the phalanges would also point in this direction. The specialization of the limb is greater than that in the Proganosauria, Choristodera or Parasuchia. It can perhaps be best compared with that of the Plesiosaurs or with the Triassic Ichthyosaurs. The humerous is, however, a little more slender medially than in the Ichthyosaurs. If the rounded ossicles are really phalanges, it is evident that the limb was no longer serviceable to any extent for land or shore locomotion but had become the specialized paddle of a purely aquatic type.

Habitat, Locomotion, Food

The remains of Thalattosaurs are known only in purely marine deposits containing little or no material of terrestrial origin. They are associated with a fauna consisting of numerous forms, both vertebrate and invertebrate, which are not known to have existed away from marine areas. In the structure of the skeleton we find the abbreviated and broadened proximal segments of the limbs, the slender snout with prehensile terminal teeth, and the median superior nares, indicating a purely aquatic type. There can scarcely be room for doubt that the Thalattosaurs as a group were typical marine forms.

The larger and more specialized species comprised in the genus *Thalattosaurus* were strictly natatory. They may have visited the shore but, like the Plesiosaurs, were better fitted for swimming than for crawling. Of the smaller *Nectosaurus* we unfortunately do not know the limbs. They may have been considerably less specialized than in the other genus, and the animal to a correspondingly greater degree a shore dweller. *Nectosaurus* is, however, found in the same deposits with the other forms and appears to be as common as the others; so that it is safe to consider it as having passed the greater part of its life away from the shore.

From what we know of the vertebral column of *Thalattosaurus* it appears that the animal had a relatively short neck and a long dorsal region, the proportions being near those in the vertebral column of some Mosasaurs. Only the anterior portion of the caudal region is known. The slender, rounded neural spines with well developed zygapophyses seen here are not such as commonly appear in forms with a highly specialized sculling tail, and it is hardly probable that a caudal fin of large size was developed.

The anterior limbs evidently formed paddles of moderate size. The posterior pair may have been larger, in compensation for lack of a strong sculling tail. It is, however, possible that as in *Geosaurus* the hind limbs were not typically natatory and that the distal end of the tail was vertically expanded.

No specimens have yet been found which are well enough preserved to show any remains of the stomach contents, and we have no definite evidence concerning the food of the Thalattosaurs, more than is furnished by the general structure of the animal. The character of the paddles, the form of the skull, and the presence of slender prehensile teeth in the terminal portions of the jaws would indicate that they fed in part upon some swiftly moving prey which was caught by a quick snap of the jaws, deglutition being assisted by the curved teeth of the pterygoid. The heavy vomerine and posterior mandibular teeth may have been used for crushing the light shells of ammonites, which existed in vast numbers in the same seas.

Affinities and Systematic Position

As would be expected in forms occurring in the Triassic, the Thalattosauria exhibit many features which are generally considered as primitive. Among these are the biconcave vertebrae, single-headed ribs, well developed abdominal rib plastron, narrow scapula, plate-like coracoid, sculptured jaw elements, strong vomerine and pterygoid dentitions, and the presence of a parietal foramen. It is, however, by no means a primitive type, but is really one of the more specialized of the reptilian groups of the Triassic. Peculiar or specialized characters appear in the structure of the limbs, in the rostral region of the skull, in the position of the narial openings, in the relations of the nasals and premaxillaries, in the character of the parietals, and in the nature of the dentition.

Owing to the considerable degree of specialization of the particular kind which we find in this group, it would almost necessarily be true that any order in which it could be placed would be comprised mainly of aquatic forms. Its relationship to any other than an aquatic group will probably be a weaker bond than ordinal affinity, and very close similarity must be sought in some of the natatory types.

The characters of the Thalattosaurs are such as to bring them into more or less definite relationship to a considerable number of groups. In some cases this is due to similar adaptation. To several quite different groups they show true affinities of nearly the same degree, indicating relationship through a common ancestral type or group from which they have all originated. The most important resemblances and affinities are discussed somewhat in detail before presenting the conclusions reached through these comparisons.

Ichthyosaurian Affinities.—The Thalattosaurs inhabited the same seas with a large group of Ichthyosaurians and showed much the same kind of adaptation carried also to a high degree. The Ichthyosaurs are generally held to be nearly related to the Rhynchocephalia, and the Thalattosaurs are evidently near relatives of that group. Under these circumstances we should expect to find the Ichthyosaurs and Thalattosaurs showing similar structure and giving evidence of near relationship.

In the extremities, where adaptation to aquatic conditions is most readily and distinctly expressed, we find both forms exhibiting the typical natatory type. In the Ichthyosaurs the propodial and epipodial elements show a somewhat greater degree of abbreviation. Unfortunately we do not as yet know the character of the terminal portions of the paddles in the Thalattosaurs and can make no comparison here. As far as is known, the ichthyosaurian paddles seem to have attained a slightly higher degree of specialization.

In the vertebrae of the two groups there are considerable differences in the character of the neural spines, in the zygapophyses and in the attachment of the upper arches to the centra. The difference in form is particularly noticeable in the anterior caudal region. The pectoral girdles are somewhat similar, but as far as is known the pelvic arches are quite different.

In the skull we find the nares occupying much the same position in both groups, and the premaxillaries are elongated in both. In the Ichthyosaurs the premaxillary elongation is extreme and the maxillaries are not only relatively small but seem actually to have suffered reduction. Distinctive skull characters separating the Ichthyosaurs widely from the Thalattosaurs are noted in the absence of an inferior temporal opening and of a coronoid elevation, the separation of the postfrontal and postorbital, the enormous size of the nasals and their different relations to the premaxillaries, the different relations of the parietals to the small frontals and to the superior temporal openings, a different structure in the palatine region, the lack of vomerine and pterygoid teeth, and the isodont or only slightly differentiated character of the gnathic dentition in all the known species of this epoch.

Some of the structural differences separating these two groups are doubtless to be correlated with difference in habits; in other words, they may be ascribed to somewhat different kinds of adaptation. The Ichthyosaurs were largely fish eaters. They therefore had no great need of a heavy vomerine dentition. In the same way the presence of a strong coronoid projection on the thalattosaurian jaw may be correlated with somewhat increased muscular power used in crushing with the broad teeth of the prevomer and of the posterior portion of the dentary. Other differences may be due to great increase in the size of the orbits in the Ichthyosaurs, although this may be considered as due to better opportunity for increase in size in that group owing to fundamental difference in the original structure of the skull.

These facts are particularly significant when we consider their bearing on questions concerning the origin and relationships of the Ichthyosaurs. If the Thalattosaurs and Ichthyosaurs were both derived from the primitive Diaptosauria and were both typical marine forms following somewhat similar lines of adaptation, why are they so different? With similar environmental conditions we would expect but little divergence. It is evident that in this case we have one of the following possibilities: 1. The Thalattosaurs and Ichthyosaurs have come from the same stock but have followed quite different lines of adaptation; 2. They have come from the same stock and have followed only slightly different lines of adaptation, but have, one or both, been in existence for a very long period; 3. They have originated in different groups.

Concerning the first possibility—there is reason to believe that the groups differed somewhat though not greatly in food habits, but that in a broad way the kind of adaptation was the same. It was such as would generally tend to produce a certain degree of convergence. The kinds of adaptation we should presume to differ less than among the Cetacea, while the structural differences are as great or greater than we find produced in not less than four periods of evolution in that more rapidly living aquatic group.

Regarding the second case—we unfortunately know as yet but little concerning the early history of either group. Thalattosaurs are known as early as the beginning of the Upper Triassic, and the oldest Ichthyosaurs which we know are found in the lower part of the Middle Triassic. The Ichthyosaurs certainly appear to be somewhat more specialized than the Thalattosaurs and are presumably somewhat older, so that we could imagine a slight difference in adaptation acting through a long period as having resulted in the production of these very different types out of the same stock. The Ichthyosaurs may have taken to the sea earlier, and the Thalattosaurs have originated from a later and therefore somewhat different phase of the same group. On the other hand the development of such differences as we see here must have required much time, and it may well be questioned whether the time of origin of the Ichthyosaurs may not date back so far that it would be straining a point to call its ancestors Diaptosaurian or even Diapsidan.

The remaining situation, in which we would have the two groups converging from fundamentally different stocks, seems in many respects the most natural relation. At any rate, the two groups must be considered as widely separated, and neither may be judged to be ancestral to the other. If they are not closely related and it should appear that of the two the Thalattosaurs are nearer to the Rhynchocephalia, we may perhaps reasonably question the rhynchocephalian or diaptosaurian origin of the Ichthyosaurs.

Parasuchian Characters.—The general skull structure of the Thalattosaurs has a certain degree of resemblance to that in *Belodon*, particularly in the rostral and temporal regions. The position of the nares is similar, as also the general form of the premaxillaries and maxillaries, though the premaxillaries do not separate the nasals and reach the frontals. The superior temporal openings are similarly situated low down between the upper temporal bars, and the parietals bound the anterior side to a greater extent than is usual. There is also some similarity in the structure of the palate, and the gnathic dentition of *Belodon* is not unlike that of *Thalattosaurus perrini.* Taken as a whole, however, the two skull types are very dissimilar. The superior nares of *Belodon* are in the large nasals; the premaxillaries do not reach back to the frontals; large antorbital vacuities are present; the lachrymals are large, while the prefrontals, frontals and parietals are relatively very small; the postorbital and postfrontal are separate; there is no pineal foramen; the form of the quadrate is very different from that of *Thalattosaurus;* the palatine borders the inferior nares externally; the coronoid is small and inferiorly situated; there are no teeth on the prevomers or pterygoids; and there is a large mandibular vacuity. These differences together with the total dissimilarity in the structure of the vertebrae, ribs and limbs show that the two groups are ordinally distinct. The general outlines of the structure in both are those of the primitive diapsidan Reptilia. Both are aquatic types and to a slight extent this has tended to bring them nearer together. The possibilities of evolution in the *marine* Thalattosauria were, however, much greater and also specifically different from those open to the *fresh water* Parasuchians, and the result of specialization has been the production of very different forms. As different as these two are, it may be noted that they are at least as near together as the Thalattosaurs and the Ichthyosaurs, although the latter are marine.

Relationship to Squamata.—Although the Thalattosaurs evidently possessed two temporal openings, with a complete lower temporal bar, their resemblance to the lacertilian and mosasaurian branches of the Squamata are so prominent as to demand consideration of possible relationship to them. The general aspect of the mandible is that of a representative of the Squamata, though it is also approached in the Rhynchocephalia. The form, situation, and prominence of the coronoid are such that the posterior portion of the jaw taken alone could scarcely be considered as other than lepidosaurian.

On the superior side of the skull there is a noticeable similarity to the Mosauria. In both the Thalattosaurs and Mosasaurs the rostral region is narrow; it is generally somewhat elongated and acute terminally. The nares are set well back and the premaxillary is produced posteriorly as a stem or bar which meets the frontals. There are no discrete nasals in the Mosasaurs and they are generally supposed to be united with the posterior end of the premaxillary bar as in *Varanus*. Should it appear that they have been lost and the fronto-premaxillary connection be immediate, the structure in this region would be very similar in the two groups.

In the posterior part of the Mosasaur skull the broad frontals are often partly arched around the anterior ends of the parietals as in the Thalattosaurs, while the postfrontal and postorbital have partly united. So far as can be determined, there is room to suppose that the upper portion of the temporal region may not differ greatly in the two groups. The quadrate of the Thalattosaurs is in general of rhynchocephalian type and the widely extended anterior wing is not seen in the Squamata, but the presence of a strong external wing and the incipient development of a posterior hook make it begin to show resemblance to the type seen in the Mosasaurs and Lizards.

In the characters of the limbs and arches there is much that is similar. The vertebrae and ribs differ, but perhaps not so fundamentally as would appear from superficial examination.

On the whole the resemblance to the aquatic Squamata is very striking; but it can not overbalance such characters as the evident presence of a lower temporal arch, the existence of a strongly developed vomerine dentition, an immovably fixed mainly rhynchocephalian quadrate, abdominal ribs and very primitive vertebrae.

While it is not possible to place the Thalattosaurs in the Squamata, as that group is at present defined, it is not improbable that the primitive Lacertilians were closely related to or derived from the land or shore forms from which the Thalattosaurs were derived. Adaptation to aquatic life would tend to make the Thalattosaurs take on rapidly a certain set of characters which would appear again in the Mosasaurs. This specialization would at the same time take the Thalattosaurs out of the direct line of evolution. It is to be noticed in this connection that the smallest and least specialized form, seen in *Nectosaurus*, is nearer the Lacertilia than the larger and more specialized *Thalattosaurus*.

In *Paliguana* Broom, of the South African Triassic, we have represented an undoubted Lacertilian with the lower temporal arch absent and only a minute process projecting from the posterior side of the jugal. The quadrate is typically lacertilian as are also the relations of the elements in the upper temporal bar. This form shows that the characteristics of the Squamata were expressed very early and makes more probable the discovery of lacertilian tendencies in early diaptosaurian groups.

Relationship to the Proganosauria.—As possible close relatives of the Thalattosaurs, the Proganosauria claim especial notice, being a group of rather primitive aquatic forms having affinities with the Rhynchocephalia and occurring earlier in geological time than the Thalattosaurs, and therefore possibly ancestral to them. Unfortunately the part of the thalattosaurian skeleton of which we have the best knowledge, viz. the skull, is the most imperfectly known part in the Proganosauria. Osborn considers the skull probably double-barred, though the structure of the temporal region is as yet unknown. The position of the superior nares and the structure of the palate are likewise unknown. Teeth are present on the roof of the mouth on what are supposed to be the palatines, while in the

Thalattosaurs they are absent from the palatines, and present on the prevomer and pterygoids. The skull is considerably longer and more slender in the Proganosauria and the long, slender teeth are more numerous.

In the structure of the better known parts of the skeleton of the Proganosaurs the separation is wide. The small centra and greatly expanded upper arches of the vertebrae and the peculiar narrow-headed ribs of the Proganosaurs stand in strong contrast to the relatively small upper arches and the broad-headed ribs of the Thalattosaurs. In the pectoral girdles of the two there is some similarity excepting in the scapula. The plate-like pelvis of the Proganosaurs is much more primitive than that of the Thalattosaurs and the limbs of the former have not gone nearly so far in specialization, particularly in the shortening and broadening of the epipodial elements.

Relationship to the Choristodera.—The aquatic diaptosaurian forms included in the Choristodera resemble the Thalattosaurs mainly in that they are aquatic and have rhynchocephalian affinities. Here, as in the Thalattosaurs, there is a vomerine dentition but the teeth are small, very numerous, of an entirely different form, and are set in several rows. The pterygoid dentition is also different and the palatines bear teeth. The Choristodera are farther distinguished from the Thalattosaurs by the more slender snout, the terminal position of the nares and the correspondingly different structure of the rostral region, the absence of a pineal foramen and of a coronoid process, the robustness of the ribs and the bicipital articulation of those in the anterior dorsal region, the different form of the elements in both pectoral and pelvic arches, and the relatively but little specialized limbs.

In the lengthening of the snout the Choristodera are more specialized than the Thalattosaurs, but the terminal position of the external nares shows the kind of specialization which we find mainly in aquatic reptiles belonging in fresh water, while the position of the nares in the Thalattosaurs is the form of specialization seen generally in marine types.

When we consider along with other things that the Choristodera are in some respects much less specialized than the Thalattosaurs, and that they occur two geological periods later, it is evident that they are not closely related.

Resemblance to Proterosuchus.—Some interesting resemblances to the Thalattosaurs are shown in *Proterosuchus* recently described by Broom.[12] This important form is known only from the anterior portion of a skull recently discovered in the Karoo beds of Tarkastad, South Africa. In it we find dentigerous prevomers and pterygoids with edentulous palatines. The prevomers reach back to meet the pterygoids broadly. On the upper side of the pterygoids are high, thin vertical plates. The characters of this form amply justify its determination by Broom as "a primitive Rhynchocephalian which shows a considerable degree of specialization along a line which gave rise to the crocodiles . . ."

The combination of characters found in *Proterosuchus* is in some respects similar to that seen in *Thalattosaurus*, and as is shown by Broom for *Proterosuchus*, the palatine region exhibits a general resemblance to that of *Procolophon*. In other characters, as in the presence of large antorbital vacuities, the anterior position of the external nares, the position of the internal nares farther forward and separated by the main bodies of the prevomers, in the absence of a coronoid process, and in the large size and heavy fangs of the slightly differentiated teeth, *Proterosuchus* shows itself to be quite different from *Thalattosaurus*. The resemblance exhibited by these forms is evidently in the main due to their approximation to the type of the primitive Rhynchocephalia. Such similarities as we find are not sufficient to permit our including them both in the same order. In adaptation to aquatic conditions *Proterosuchus* might have led to some such forms as the Parasuchians, while the Thalattosaurs stand as a type very different from this order.

Relationship to the Proterosauria.—Very close affinity with any of the forms in this order is precluded by the totally different structure and function of the limbs, the character of the pelvis, and to a considerable extent also of the lower jaw and the facial region.

The skull of *Palaeohatteria* differs from that of the Thalattosaurs in the terminal position of the superior nares, the small and short premaxillaries, large maxillaries and lachrymals, very large nasals, separate postfrontal and postorbital, absence of coronoid or at least of a prominent coronoid projection, and in the presence of large prehensile teeth on the posterior portion of the jaws. It might be presumed that the greater number of these differences could be brought about by retrogression of the narial openings with corresponding enlargement of the premaxillaries, in the evolution of an aquatic form from a type originally like *Palaeohatteria.* There are, however, few real similarities connecting *Palaeohatteria* and the Thalattosaurs which would not at the same time show affinities with the majority of the older diapsidan orders. While such modification may be considered possible, there is nothing to show that it has actually occurred.

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[12] R. Broom, Ann. South African Mus. v. 4, art. 7, p. 159, pl. xix. Nov. 1903.

The relationship to *Proterosaurus* is hardly nearer than to *Palaeohatteria.* The limbs, girdles and vertebrae are very different, and the skull is not more similar. The facial region in some respects seems to present a stronger resemblance than to *Palaeohatteria* and if, as Seeley has suggested, the openings immediately in front of the orbits in *Proterosaurus* are really the superior nares, there would be an important feature common to the two. The nasals are, however, very large, reaching far forward as in the Ichthyosaurs, and the premaxillaries appear to have no posterior stem. In the palatine region we find the prevomer long and slender, and the palatines swinging around the narial openings and coming into broad contact with the prevomers in front of the nares as well as behind them.

Evidently no close affinities are to be found with the Proterosauria, and while we must suppose the Thalattosaurs to be derived from Permian land or shore forms, it would not be possible to unite them with this group or even to consider the Proterosauria as the ancestral type. As has been shown by Seeley, Nopcsa, Osborn and others the trend of evolution in the Proterosauria was already decidedly toward the development of specialized land forms, as seen in the Dinosauria.

The Thalattosaurs are probably derived from land forms, as is evidenced by the character of the pelvis and of the neural spines of the vertebrae. The Proterosaurs probably come nearer than any other group to this primitive type, but are not themselves the ancestral forms which we seek.

Relationship to the Rhynchocephalia.—In a large number of the skeletal characters, strong similarities to the Thalattosaurs are found in various members of the Rhynchocephalia. In the general plan of the skull there are many points of resemblance, and the uniformity of this resemblance throughout the various parts is particularly noticeable. In some respects we find in the Rhynchocephalia approximations to thalattosaurian characters not seen elsewhere.

In the superior temporal region the similarity of *Sauranodon* and *Pleurosaurus* to the Thalattosaurs is evident. The parietals here extend around the anterior ends of the upper fenestrae as in *Belodon*, and in both of these genera they meet the squamosals on the outer side of the upper temporal openings.

In the structure of the arches and ribs many common characters are found, although the vertebrae are not closely similar. The similarity of the more slender pelvic elements is particularly noticeable, being closer than between the thalattosaurian elements and the primitive plate-like pelvis of the Proterosauria and Proganosauria or the broad pelvic elements of the Choristodera.

As discriminating characters, we find that no true Rhynchocephalian possesses a vomerine or pterygoid dentition or shows the degree of adaptation of the limbs and skull to aquatic conditions that we find in the Thalattosaurs. No member of this order has such highly specialized limbs and in none do we find the thalattosaurian structure of the rostral region. *Pleurosaurus* and *Acrosaurus* were aquatic forms, but the limbs were only slightly modified. The structure of the nasal region in *Pleurosaurus* approaches that of the Thalattosaurs but does not appear to be the same. Moreover, in *Pleurosaurus* where we find some of the closest resemblances, the structure of the lateral temporal region appears very different. From Lortet's figures[13] it would seem that there is no lateral temporal vacuity here. Such was also the impression obtained by the writer in a hasty examination of his specimen.

As all of the Rhynchocephalia which we have for comparison are much younger than the Thalattosaurs, and are all in many respects less specialized, it is useless to attempt to place them in any very close relationship to the Thalattosauria. It is probable that they are derived from a persistent land or shore type from which the Thalattosaurs are an early offshoot.

Conclusions

From the comparisons that have been made, it is evident that the Thalattosaurs are to be considered as an independent group.

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[13] Rept. Foss. du Bassin du Rhône, 1892. Pl. VIII, figs. 1 and 2.

The orders with which they have most in common are either those comprising typical aquatic forms or those in which rhynchocephalian characters are very prominent. Even where we have the characters of an aquatic animal developed in a form of the rhynchocephalian type, we fail in every instance to find closer affinity than the bond between the Mosasauria and the Lacertilia or that between the Choristodera and the Rhynchocephalia.

During the period in which the Thalattosaurs flourished there were three other important groups of marine reptiles in existence. These were the Nothosaurs, Ichthyosaurs and Placodonts, none of which were closely related to the Thalattosauria. Of the older reptilian orders, the Proterosauria and Proganosauria are nearest the Thalattosaurs. The first of these comprises terrestrial types with quite a different structure and showing already in the Permian that the tendency of their evolution was toward highly specialized land forms. The Proganosaurs, also of the Permian, exhibited a different type of evolution in the skull, ribs and vertebrae, and had much less specialized limbs.

Of the younger orders the Choristodera and Rhynchocephalia show noticeable similarity to the Thalattosaurs in their fundamental skeletal plan. The affinity with the Choristodera is on the whole weak, as the skull, arches and limbs are decidedly different. They represent a distinct aquatic type which must reach back to the primitive Diaptosauria for a true expression of its affinity with the Thalattosaurs. The Rhynchocephalia s. str. as shown in the numerous types ordinarily classed in it show more real kinship with the Thalattosaurs than most of the other orders. Affinities are expressed in varying degrees in *Sphenodon*, *Homeosaurus*, *Pleurosaurus* and *Sauranodon*. It is, however, to be doubted whether all of these forms should be grouped in one order. In the possession of numerous peculiar characters, both primitive and specialized, and particularly through the group of characters which has arisen owing to the higher degree of adaptation to aquatic conditions, the Thalattosaurs show themselves distinctly separated from the true Rhynchocephalia.

The resemblances to the Squamata are striking. They are evidently founded in a large measure on parallelism, but may also be due to close affinity between the primitive Thalattosaurs and the particular group in the primitive Diaptosaurs from which the Squamata originated.

The Thalattosaurs represent an early adaptation to marine conditions of that division of the Reptilia which has persisted in measurably primitive form in the Rhynchocephalia. During the early history of that group it gave rise to a numerous company of forms taking quite divergent paths in their evolution. Of the older orders only the Proganosauria were aquatic. They appear, however, to have been limited to fresh water. The Thalattosaurs are evidently the marine representatives of this great rhynchocephalian or diaptosaurian group. In accommodation to marine conditions their specialization toward the natatory type was carried farther than it would naturally go in forms living in the more narrowly circumscribed bodies of fresh water. In sea forms a continued or sustained existence in the water, and even some distance away from the shore, was probably advantageous. Such a tendency would necessarily result in the evolution of the only type of extremity that would be serviceable; namely, the paddle. In bodies of fresh water where the shore is in general easily accessible the functions of the limbs would be divided between crawling and swimming.

Of the seven orders tentatively placed in the Diaptosauria by Osborn none are composed of typical natatory, marine forms. It would have been remarkable had there not been developed in the adaptive expansion of this group just such a type as is represented here. In the relation of the Thalattosaurs to the other diaptosaurian orders we find a situation similar to that in the Squamata, the Thalattosaurs showing the same kind of adaptive specialization away from the primitive Diaptosauria that the Mosasaurs have exhibited with relation to the primitive Lacertilia.

Generic and Specific Characterizations

In general, the structure of the known specimens indicates close relationship of the forms which they represent. There is, however, a certain degree of variation, particularly of the dentition and limbs, which is best expressed by separating them into two or more genera.

THALATTOSAURUS *Merriam*

Bull. Dept. Geol. Univ. Calif. v. 3, no. 21, p. 419.

Type species, *Thalattosaurus alexandrae.*

Posterior mandibular teeth, broad-elliptical in cross-section, low-crowned; median teeth increasing in height anteriorly through the development of an antero-external tubercle. Anterior mandibular and premaxillary teeth slender conical. Maxillary teeth conical in one species, imperfectly known in the others. Humerus short, expanded distally, with high pectoral ridge. Radius and ulna much shortened.

Thalattosaurus alexandrae *Merriam*

Plates I, II; Plate IV, Fig. 1; Plate V, Figs. 1*a*–2*b*; Plate VI; Plate VII, Figs. 1–3, 8–9; Plate VIII, Figs. 1–2, 4*a*–6

Bull. Dept. Geol. Univ. Calif. v. 3, no. 21, p. 419.

Type specimen No. 9085 Univ. Calif. Palae. Coll.

This is the largest species of the group. The known specimens appear to represent individuals attaining a length not far from two metres. Neural spines of vertebrae not greatly widened. Propodial and epipodial limb elements and scapula considerably expanded. Nasal openings long, portion of nasal elements behind the nares relatively short. Slender anterior teeth with widely spaced striae. Posterior mandibular teeth very low-crowned, button-like. The number of teeth on the dentary appears to have been eighteen.

A large part of our knowledge of the Thalattosauria has been obtained through the study of this species, of which several representative specimens are known. All of the material representing this form has been obtained in the Trachyceras horizon of the Hosselkus Limestone. No occurrences are known outside the Shasta region of California.

Measurements

Vertebrae

	mm.
Anterior dorsal (No. 9084), height of centrum	20
“ “ “ width “ “	23
“ “ “ length “ “	16
“ “ “ height of upper arch	46
“ “ “ antero-posterior diameter of upper arch at middle height of spine	13
“ “ “ transverse diameter of upper arch at middle height of spine	[14]*a*5
Anterior caudal (No. 9085), height of centrum	30
“ “ “ width “ “	13
“ “ “ length “ “	18

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[14] *a*, approximate.

			mm.
Anterior caudal	(No. 9085),	height of upper arch	48
“	“	“ antero-posterior diameter of upper arch at middle height of spine	8
“	“	“ transverse diameter of upper arch at middle height of spine	6
		Arches	
Coracoid	(No. 9085),	antero-posterior diameter	65
“	“	transverse diameter of median portion	33
Scapula	“	greatest length	55
Ischium (?)	“	“ “	72
“	“	“ width	26.5
Pubis (?)	(No. 9044),	“ length	106
“	“	“ width	47
		Limbs	
Humerus	(No. 9084),	greatest length	75
“	“	“ width, proximal end	39
“	“	“ “ median portion	21
“	“	“ “ distal end	52
“	“	“ thickness of distal end	18.5
Radius	“	“ length	*a*40
“	“	“ width, distal end	*a*29
“	“	“ “ median portion	15.5
Ulna	(No. 9085),	greatest length	40
“	“	width, median portion	25

Thalattosaurus shastensis, n. sp.

PLATE III; PLATE IV, FIGS. 2*a–c;* PLATE VII, FIGS. 4, 7; PLATE VIII, FIGS. 3, 7, 8

Type specimen No. 9120 Univ. Calif. Palae. Coll.

Compared with *T. alexandrae* the individuals are considerably smaller; the scapula, humerus and ulna more slender; the nasal openings shorter and that portion of nasal bones behind the openings longer and broader; the neural spines of the dorsal vertebrae are possibly shorter. The conical teeth associated with the type specimen show more numerous and more closely set longitudinal striae than are seen in the jaw teeth of *T. alexandrae.* There is of course a possibility that these teeth belong to the pterygoids and not to the jaws.

This species appears to be very near the type form of the genus and may be shown later to be identical with it, possibly representing young individuals. There are, however, several specimens in the collection which seem to have the same characters and to be slightly removed from *T. alexandrae.*

This form is not uncommon, and ranges from the Trachyceras horizon almost if not quite to the top of the Hosselkus Limestone. It is known only from the Triassic of Shasta County.

MEASUREMENTS

	mm.
Humerus (No. 9120), length	32
Ulna " "	21
" " greatest width	11

Thalattosaurus perrini, n. sp.

PLATE IV, FIG. 3; PLATE V, FIG. 3; PLATE VII, FIG. 6

Posterior mandibular teeth with laterally compressed and obtuse but not greatly depressed crowns, grading anteriorly into a slender conical form on the anterior portion of the jaw. Maxillary teeth slender conical, set in deep pits.

The dentition of the dentary and the maxillary are well shown. The dentary holds an interrupted series of twelve teeth with spaces for several more among them. The entire number has probably been sixteen to eighteen. The posterior ones have low, broad, laterally compressed crowns. The individuals in the middle of the series were short, broad, and leaf-like, their margins being very close together. The anterior members of the series have a shorter antero-posterior diameter, higher crowns, and a slender conical form without lateral compression. The most anterior tooth, seen only in oblique section, shows strong longitudinal striations or ridges on its surface. The most posterior teeth are close together and in shallow pits. The anterior ones are deeply set and are more widely spaced.

On the maxillary there are five teeth of slender conical form, with spaces for one or two more. They are in deep, distinct pits.

As much of the vomerine dentition as is known is very similar to that of *Thalattosaurus alexandrae.*

The general characters of this form are those of a typical Thalattosaurian.

The type specimen, the only known specimen of this species, was the first Thalattosaurian discovered. It was found by Professor James Perrin Smith in the Trachyceras beds of the Hosselkus Limestone at Smith Cove, near Squaw Creek, Shasta County. There was exposed on the slab only a prevomer with its peculiar, blunt teeth. Later the portion of the skull shown on Plate IV, figure 3, was exposed by preparation with steel points and by etching with very dilute hydrochloric acid. After the jaws had been partly uncovered, the writer published a note on the Triassic Reptilia from Northern California,[15] in which this specimen was referred to as a *Shastasaurus* with a heterodont dentition. Later it was discovered that it could not belong to the Ichthyosauria, but the true affinities were not known until after the discovery and study of the type of *Thalattosaurus alexandrae*.

This species is quite distantly removed from *T. alexandrae* in dental characters, and may be found to represent a distinct genus.[16] Although the posterior mandibular teeth differ much from those of *T. alexandrae* the difference is only one of degree. So far as known the character of the maxillary teeth seems to be quite different both as regards form and insertion. Satisfactory comparison can not be made, however, until we know more of the dentition of *T. alexandrae*.

NECTOSAURUS, n. gen.

Nectosaurus halius, n. gen. and sp.

PLATE IV, FIG. 4*a*–5; PLATE V, FIGS. 4, 6; PLATE VII, FIG. 5

Type specimen No. 9124 Univ. Calif. Palae. Coll.

Fronto-parietal region similar to that of *Thalattosaurus*. Quadrate with exterior wing. Mandible of lacertilian type. Crowns of posterior mandibular teeth conical, acute, slightly recurved, coarsely striated.

To this species are referred a portion of a skull constituting the type, and a number of isolated bones which seem to belong here. The type was the first thalattosaurian specimen to be carefully studied. Manuscript was originally prepared for its description as a primitive lacertilian but was withheld from publication until more material should be obtained.

While the mandible and quadrate are of a lacertilian type, thalattosaurian affinities are indicated by the character of the fronto-parietal region. The frontals (Pl. IV, fig. 4*a*) have the same form as in *Thalattosaurus.* They receive the premaxillaries between them anteriorly, and clasp the parietals posteriorly. There is also present a portion of a prefrontal and a post-fronto-orbital. A cross-section of a vertebra (Pl. VII, fig. 5) shows the upper arch apparently firmly connected with the centrum.

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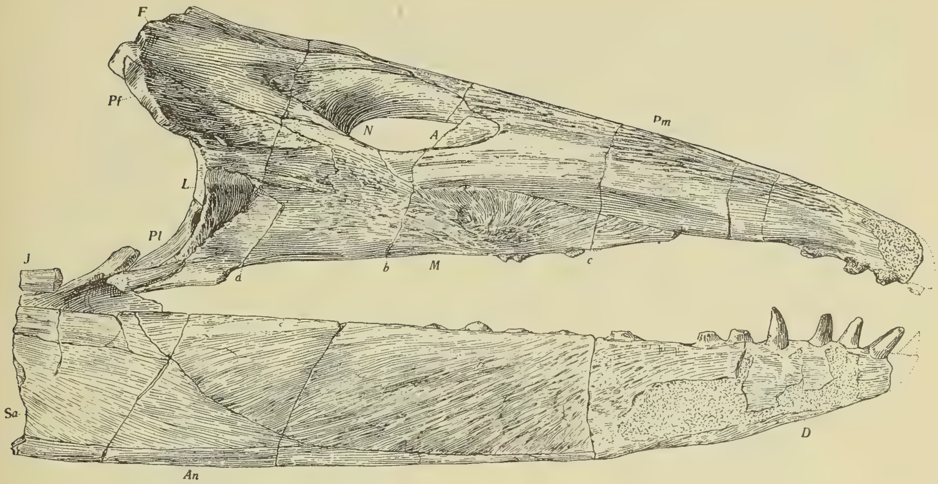
[15] Science, n. ser. v. 15, p. 411.

[16] Should this type be found to be generically distinct from *Thalattosaurus* the generic name *Scenodon* will be used to distinguish it.

This genus contains the most primitive forms of the Thalattosauria and will probably furnish additional evidence concerning their relationships when its skeletal structure is better known.

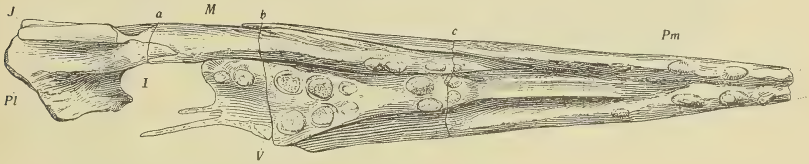
N. halius appears to be present at nearly all horizons of the Hosselkus Limestone.

In Plate V, figure 6, there is shown a small jaw representing a type quite common in the Hosselkus Limestone. While not seen in association with certainly recognizable *Nectosaurus* remains, it is doubtfully referred to that genus. The dentigerous palatal element shown in Plate V, figure 4, is still more doubtfully determined as belonging here.



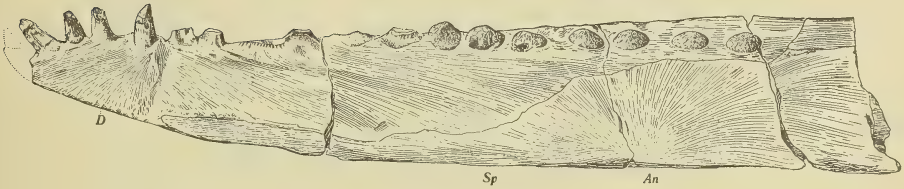
1

Anterior portion of cranium and mandible. Cranium slightly distorted, the anterior end of the maxillary being covered.



2

Palatal view of cranium



3

Inner side of mandible

Thalattosaurus alexandrae

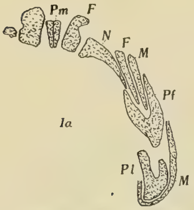
Type specimen. All figures one half natural size

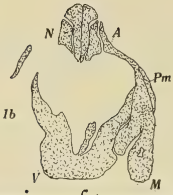
F, frontal
Pf, prefrontal
N, nasal
A, doubtful element anterior to narial opening
Pm, premaxillary

M, maxillary
L, lachrymal
Pl, palatine
J, jugal
V, prevomer
I, inferior narial opening

Sa, supra-angular
An, angular
D, dentary
Sp, splenial
a, *b*, *c*, sections of cranium. See Pl. II, figs. 1*a*, 1*b*, 1*c*.

N and A in fig. 1 are situated in the superior narial opening.





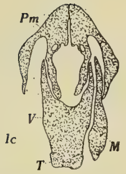
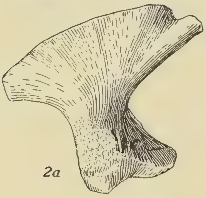


FIG. 1*a*. Section *a* through cranium of type specimen, posterior to superior nares. See Pl. I, figs. 1 and 2, section *a*.

FIG. 1*b*. Section *b* through cranium of type specimen, anterior portion of superior narial region. See Pl. I, figs. 1 and 2, section *b*.

FIG. 1*c*. Section *c* through cranium of type specimen, middle rostral region. See Pl. I, figs. 1 and 2, section *c*.



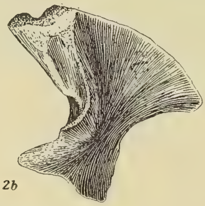
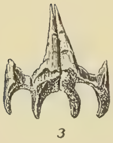


FIG. 2*a*. Right quadrate, inner side.
FIG. 2*b*. Right quadrate, outer side.



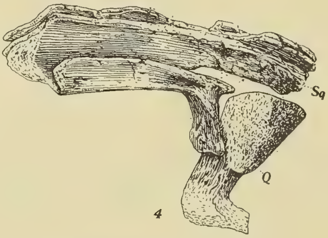
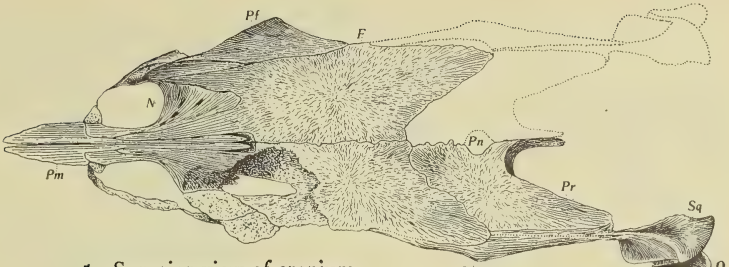


FIG. 3. Posterior end of premaxillary. *T. alexandrae* (?).
FIG. 4. Fragment of quadrate and temporal region of type specimen.

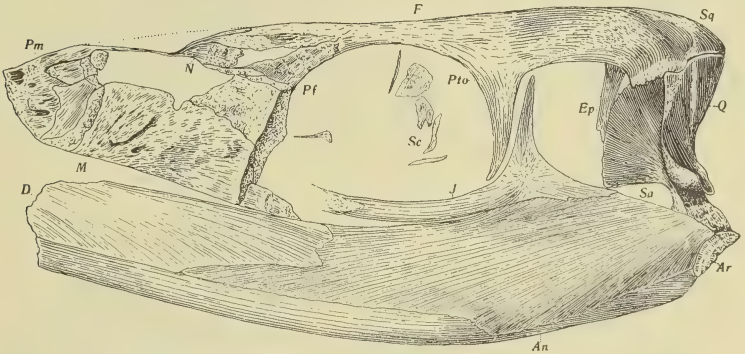
Thalattosaurus alexandrae

All figures one half natural size

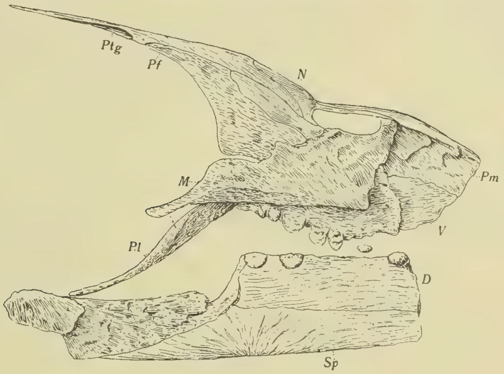
M, maxillary
Pm, premaxillary
N, nasal
F, frontal
Pf, prefrontal
A, doubtful element anterior to narial opening
Pl, palatine
V, prevomer
T, tooth
Q, quadrate
Sq, squamosal


Pf
F
N
Pm
Pn
Pr
Sq
Q
Pto

1 Superior view of cranium


F
Sq
Pm
N
Pf
Pto
Ep
Q
Sc
M
D
J
Sa
Ar
An

2 Lateral view of cranium and mandible


Ptg
Pf
N
Pm
M
V
Pl
D
Sp

3 Lateral view of skull from right side

Thalattosaurus shastensis

All figures one half natural size

M, maxillary
Pm, premaxillary
N, nasal
F, frontal
Pr, parietal
Pn, pineal foramen
Pf, prefrontal

Pto, post-fronto-orbital
Ptg, groove for post-fronto-orbital
J, jugal
Sc, sclerotic plates
Sq, squamosal
Q, quadrate
Ep, epipterygoid (?)

Pl, palatine
V, prevomer
Ar, articular (?)
An, angular
Sa, supra-angular
D, dentary
Sp, splenial

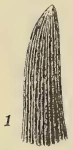


FIG. 1. Anterior jaw tooth associated with type specimen of *T. alexandrae*. Natural size.

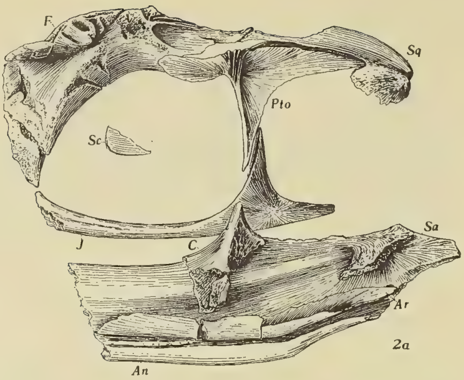
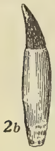


FIG. 2*a*. *Thalattosaurus shastensis*. Inner side of right half of cranium and mandible. Type specimen. ×½.



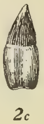
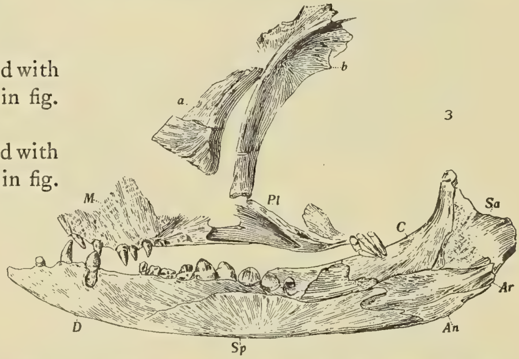


FIG. 2*b*. Tooth associated with skull of *T. shastensis* shown in fig. 2*a*. ×1⅓.

FIG. 2*c*. Tooth associated with skull of *T. shastensis* shown in fig. 2*a*. ×1⅓.



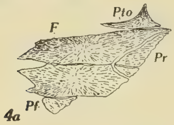
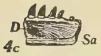
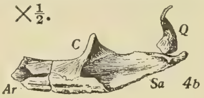


FIG. 3. *Thalattosaurus perrini*. Inner side of right half of cranium and mandible. Type specimen. ×½.

FIG. 4*a*. *Nectosaurus halius*. Superior aspect of fragment of cranium. Type specimen. ×½.





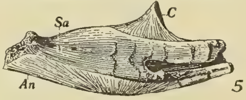


FIG. 4*b*. *N. halius*. Inner side of right ramus of mandible. Type specimen. ×½.

FIG. 4*c*. *N. halius*. Outer side of middle portion of left ramus of mandible. Type specimen. ×½.

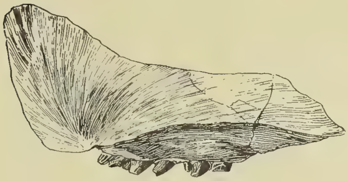
FIG. 5. *N. halius*. Outer side of right ramus of mandible. ×½. The anterior end of the supra-angular has been weathered through.

LEGEND

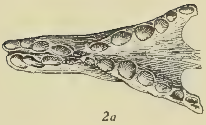
D, dentary
C, coronoid
An, angular
Sa, supra-angular
Ar, articular
Sp, splenial

F, frontal
Pf, prefrontal
Pto, post-fronto-orbital
Sc, sclerotic plate
J, jugal
Pr, parietal

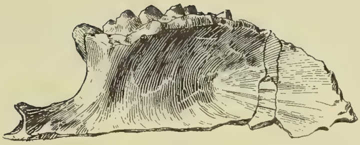
Sq, squamosal
Q, quadrate
M, maxillary
Pl, palatine
a, prefrontal (?)
b, frontal (?)



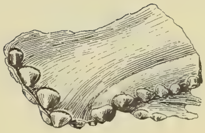
1a



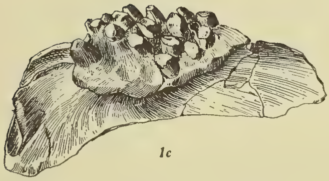
2a



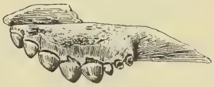
1b



2b



1c



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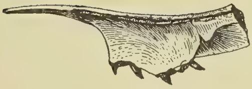

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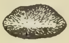

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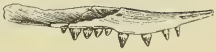


6

FIG. 1*a*. *Thalattosaurus alexandrae*. Pterygoid, lateral view. Type specimen. ×$\frac{2}{3}$.

FIG. 1*b*. Upper side of specimen shown in fig. 1*a*. ×$\frac{2}{3}$.

FIG. 1*c*. Lower side of specimen shown in fig. 1*a*. ×$\frac{2}{3}$.

FIG. 2*a*. *Thalattosaurus alexandrae*. Lower side of prevomer. ×$\frac{1}{2}$.

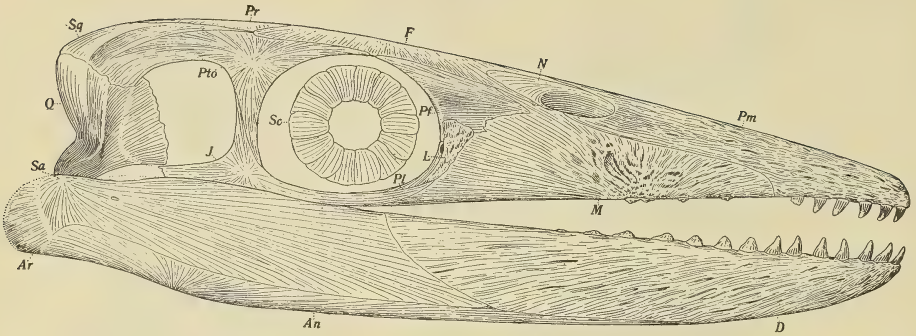
FIG. 2*b*. Lateral view of specimen shown in fig. 2*a*. ×$\frac{1}{2}$.

FIG. 3. *Thalattosaurus perrini*. Lateral view of prevomer. Median pair of teeth partly restored. Type specimen. ×$\frac{1}{2}$.

FIG. 4. *Nectosaurus halius* (?). Pterygoid or palatine, superior view. Natural size.

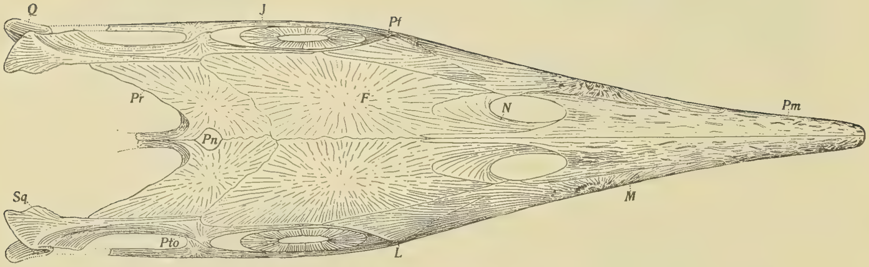
FIG. 5. *Thalattosaurus*, sp. Vomerine tooth. Natural size.

FIG. 6. *Nectosaurus halius* (?). Maxillary. ×$\frac{2}{3}$.


Sq
Pr
F
Pto
N
Q
Sc
Pf
Pm
J
L
Sa
Pl
M
Ar
An
D

1

Lateral view


Q
J
Pf
Pr
F
N
Pm
Pn
Sq
M
Pto
L

2

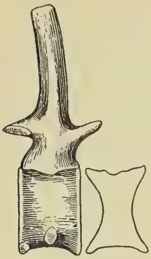
Superior view

Thalattosaurus alexandrae

Reconstruction of the skull. The temporal and fronto-parietal regions and a portion of the mandible are restored from *T. shastensis.*

About one third natural size

Pm, premaxillary
M, maxillary
N, nasal
F, frontal
Pr, parietal
Pn, pineal foramen
Pf, prefrontal
Pto, post-fronto-orbital
J, jugal
L, lachrymal
Pl, palatine
Sc, sclerotic ring
Sq, squamosal
Q, quadrate
Ar, articular
Sa, supra-angular
An, angular
D, dentary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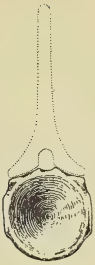
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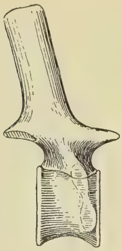
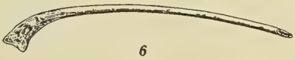

1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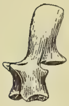
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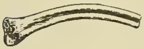
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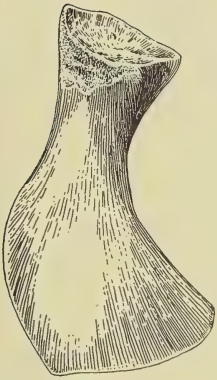
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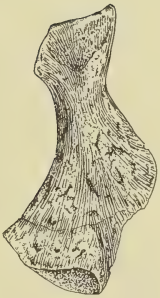
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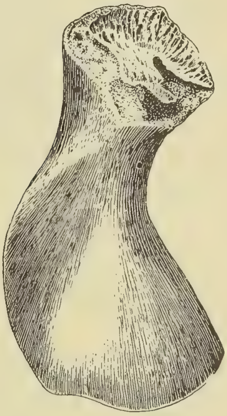

10

All figures one half natural size

FIG. 1. *Thalattosaurus alexandrae.* Anterior dorsal vertebra, side view.

FIG. 2. *T. alexandrae.* Dorsal vertebra, anterior side.

FIG. 3. *T. alexandrae.* Anterior caudal vertebra, side view and sagittal section. The neural spine appears to be somewhat too erect in the figure. Type specimen.

FIG. 4. *T. shastensis.* Neural arch of a cervical or anterior dorsal vertebra. Type specimen.

FIG. 5. *Nectosaurus halius.* Weathered cross-section of vertebra. Type specimen.

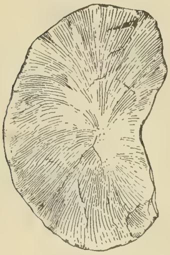
FIG. 6. *Thalattosaurus perrini.* Anterior dorsal rib. Type specimen.

FIG. 7. *T. shastensis.* Head of dorsal rib. Type specimen.

FIG. 8. *T. alexandrae.* Pubis (?).

FIG. 9. *T. alexandrae.* Ischium (?). Type specimen.

FIG. 10. *T. alexandrae.* Pubis (?).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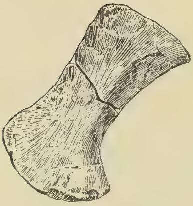
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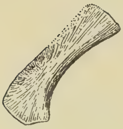
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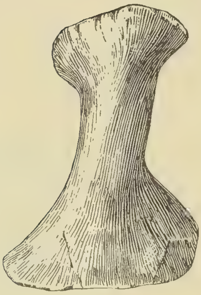
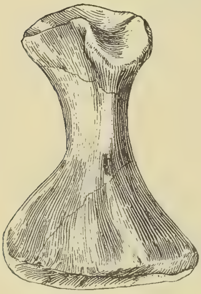

4a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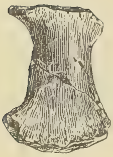
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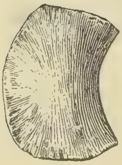
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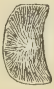
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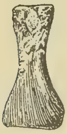
8

All figures one half natural size

Fig. 1. *Thalattosaurus alexandrae.* Coracoid. Type specimen.
Fig. 2. *T. alexandrae.* Scapula. Type specimen.
Fig. 3. *T. shastensis.* Scapula. Type specimen.
Fig. 4*a*. *T. alexandrae.* Left humerus, superior view.
Fig. 4*b*. Inferior view of specimen shown in fig. 4*a*.
Fig. 5. *T. alexandrae.* Radius.
Fig. 6. *T. alexandrae.* Ulna. Type specimen.
Fig. 7. *T. shastensis.* Ulna. Type specimen.
Fig. 8. *T. shastensis.* Humerus. Type specimen.

THE OCCURRENCE OF ICHTHYOSAUR-LIKE REMAINS IN THE UPPER CRETACEOUS OF WYOMING

THROUGH the kindness of Professor S. W. Williston, I have recently received two fragmentary vertebræ found by Mr. W. H. Reed in the Benton Cretaceous near the north end of Medicine Bow Mountains. Although very fragmentary, these vertebræ appear to represent a genus allied to *Ichthyosaurus*. As this reptilian group has not been known in North America in beds as late as the Benton, the discovery is of considerable interest.

The larger fragment consists of the upper three fourths of a deeply biconcave vertebral centrum apparently from the cervical or anterior dorsal region. The centrum is very thin antero-posteriorly, and in this respect somewhat resembles the corresponding centra in *Baptanodon discus*. The sides are considerably damaged, so that it is not possible to make a definite statement concerning the rib articulation, but it seems to have been double, as in *Baptanodon*. A foramen close to the upper end of the diapophyses is larger than any I have seen in this position in the typical Ichthyosaurs, and adds somewhat to the difficulty of making a definite determination of the relationships of this form.

When more material is available it will be interesting to learn whether this form really represents a true *Ichthyosaurus* or possibly a more highly specialized form of *Baptanodon* than those which we know from the Baptanodon beds. Should it be *Baptanodon*, it will probably show some extreme specializations, as the time separating the Benton from the Baptanodon beds is considerable.

Science, n. s., vol. 22, no. 568, pp. 640–641, November 17, 1905.

REVIEW OF "OSTEOLOGY OF BAPTANODON (MARSH)," BY C. W. GILMORE

2. *Osteology of Baptanodon* (Marsh); by C. W. Gilmore. Memoirs of the Carnegie Museum, Vol. II, No. 2, August, 1905—Mr. Gilmore's excellent paper gives us for the first time a satisfactory discussion of the osteological structure of the Jurassic Ichthyosauria of America. Notes by Marsh and Knight have acquainted us with the essential characters of the paddles, but little information concerning the remainder of the skeleton has been published, and investigators working on related groups have had no satisfactory basis for comparison with these important forms. The specimens studied by Mr. Gilmore include practically all of the known *Baptanodon* material. The figures presented represent the complete structure of the skull in all its aspects, the pectoral girdle, the anterior limb, and the anterior portion of the vertebral column. The posterior limb is not certainly known.

The characters of the dentition of *Baptanodon*, for the original discovery of which we are indebted to Mr. Gilmore, have been summed up in the statement that: "*Baptanodon* was well provided with comparatively small, somewhat slender but functional teeth that extended along the full length of the jaw; the most anterior ones being much reduced." In addition to the characters of the dentition, Mr. Gilmore notes specializations in the reduction of the cervical intercentra to a simple free element in *B. marshi*, the median fusion of the clavicles, and the presence of a sixth digit in the anterior limb.

In the comparison of *Baptanodon* with the European *Ophthalmosaurus*, the two are shown to be remarkably similar. Distinguishing characters are found in the presence in *Baptanodon* of a sixth digit in the anterior limb, the uniform biconcave cupping of the anterior cervical centra, and the fusion of the clavicles. The two types are, however, very close together, as similar as one could

American Journal of Science, ser. 4, vol. 20, pp. 403–404, November 1905.

reasonably expect to find species so widely separated geographically.

In the light of what is actually known, the relation of *Baptanodon* to the later Triassic forms of America seems still far from close. *Shastasaurus*, the youngest known Triassic genus, is at least in limb structure highly specialized along a line almost diametrically opposite that taken by *Baptanodon*. Unless a closer connection with the late Triassic forms of this continent can be discovered, we must continue to look upon *Baptanodon* as probably a Jurassic immigrant from the old world. The close relationship to the European *Ophthalmosaurus* is additional evidence in favor of the suggestion that *Baptanodon* was a Jurassic importation. In this connection it is interesting to note that Fraas[1] has recently described a vertebra which he believes to represent the genus *Ophthalmosaurus*, from the Jurassic of Northeast Greenland.

[1] E. Fraas, Meddelelser om Grönland, xxix, p. 283.

PRELIMINARY NOTE ON A NEW MARINE REPTILE FROM THE MIDDLE TRIASSIC OF NEVADA

In the summer of 1902 a joint expedition from Stanford University and the University of California visited the Middle Triassic outcrops of the West Humboldt Range in Nevada to explore these beds for palaeontological material. Mr. V. C. Osmont, who represented the University of California, devoted himself to the search for vertebrate remains. He was fortunate in obtaining a number of reptilian specimens, which furnished the first satisfactory information concerning the nature of the marine saurians known to occur there.[1] The greater part of the material obtained by Mr. Osmont consisted of remains referable to ichthyosaurian forms.[2] Associated with the ichthyosaurs is a single specimen representing a form which does not closely resemble any described reptilian type. This specimen consists of several anterior cervical vertebrae, the greater part of a mandible with the dentition, and the inferior portion of the cranium. In collections obtained later from the same locality there are several fragmentary specimens showing similar structure. The peculiar features of this specimen separate it from other forms as a distinct genus and species, possessing the following characters.

Omphalosaurus nevadanus, n. gen. and sp.

Pls. 8 and 9, and Text-fig. 1

Anterior vertebral centra biconcave. Rami of the mandible rapidly uniting anteriorly in a strong symphysis. Splenials broad and heavy. Dentaries united medially only a short distance in front of their posterior extremities, broad superior surface set with several rows of very low-crowned crushing teeth. Palatine region

University of California Publications, Bulletin of the Department of Geology, vol. 5, no. 5, pp. 71–79, pls. 8, 9, December 7, 1906.

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[1] J. Leidy, Proc. Philad. Acad. Sc., Vol. 20, p. 177; and J. C. Merriam, Bull. Dept. Geol. Univ. Calif., Vol. 3, p. 107.

[2] A Primitive Ichthyosaurian Limb from the Middle Triassic of Nevada. J. C. Merriam, Bull. Dept. Geol. Univ. Calif., Vol. 4, p. 33.

with broad edentulous pterygoid elements. Posterior portion of the palatines also apparently edentulous.

The vertebrae present are distinctly amphicoelous and the centra are nearly circular in vertical cross-section. They are in series at the back of the skull, and are evidently anterior cervicals.

The mandible has lost the articular region and is broken off a short distance in front of the symphysis. The angular, supra-angular, dentary and splenial are represented, with possibly some portions of other elements. The thickness of the jaw back of the symphysis is almost as great as the height. The rami unite in a very wide symphysis only a short distance in front of the posterior end of the dentaries. The angular extends unusually far forward between the splenial and the dentary. The heavy supra-angular shows no coronoid elevation; and no discrete coronoid element has been certainly recognized, though possibly present. As will appear from the discussion of the dentition, the development of a large coronoid elevation would almost have been expected to occur here, as in *Placodus*.

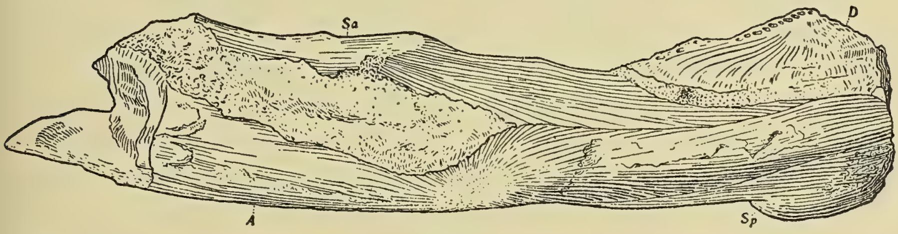


Fig. 1. *Omphalosaurus nevadanus*, n. gen. and sp. Outer side of a portion of the right ramus of the mandible. *A*, angular; *Sa*, supra-angular; *D*, dentary; *Sp*, splenial. Middle Triassic, marine beds, South Fork of American Cañon, West Humboldt Range, Nevada. About one-third natural size.

The heavy splenials extend posteriorly only a short distance behind the dentaries before they begin to thin out rapidly. Anteriorly they are suddenly widened to meet in the symphysis. The transverse diameter of the splenials at the symphysis is more than twice their width behind this region. In front of the symphysis the splenials extend downward to form a part of the lateral face of the jaw.

The dentaries extend backward a short distance over the anterior ends of the supra-angulars, and are also in contact inferiorly with the anterior extension of the angular. Like the splenials, the dentaries are much expanded transversely in the symphysial region. The posterior ends extend backward as wing-like projections for a short distance behind the symphysis.

Situated on the dentaries are numerous small, button-like teeth, somewhat similar to those of some of the pycnodont fishes. The crowns are circular in cross-section, and the elevation is considerably less than the transverse diameter. There are at least three rows of teeth preserved on the right dentary, parallel with the median border. On the left dentary, teeth extend from the median line more than half of the distance to the outer margin, and appear to have been in numerous rows. The surface of the dentigerous area seems to have been convex.

A portion of the palatine region is fairly well exposed in the lower view of this specimen (pl. 9). The two large elements separated posteriorly, but uniting medially opposite the posterior ends of the splenials, are evidently pterygoids. Anterior to them on either side are apparently the palatines. Extending backward from a point a little in advance of the middle of the pterygoids is a median space which possibly represents the posterior nasal opening. On the superior side of the specimen (pl. 8) the structure is more indistinct. One of the palatine elements appears, *viz.:* a part of one of the pterygoids. In addition to this, two heavy bones (*a*) with lateral notches are situated just behind the symphysis. Posterior to these is a large expanded element (*b*), and a large emarginate bone (*c*). The flat posterior element may belong to the roof of the cranium. The laterally notched anterior bones might be vomers, or possibly premaxillaries. The large crescentic bone may pertain to the postorbital region.

The groups of reptiles which this form most closely resembles in adaptation, so far as this is expressed in the structure of the parts present, are the Placodonts and the Rhynchosaurs. Both of these groups occur in the Trias, as does this form. The Placodonts were marine, and lived in approximately the same epoch as *Omphalosaurus*; the Rhynchosaurs were probably somewhat later in appearance, and were not typical aquatic animals. Both types differ from *Omphalosaurus* in the character of the mandibular dentition and in the structure of the skull, so far as known.

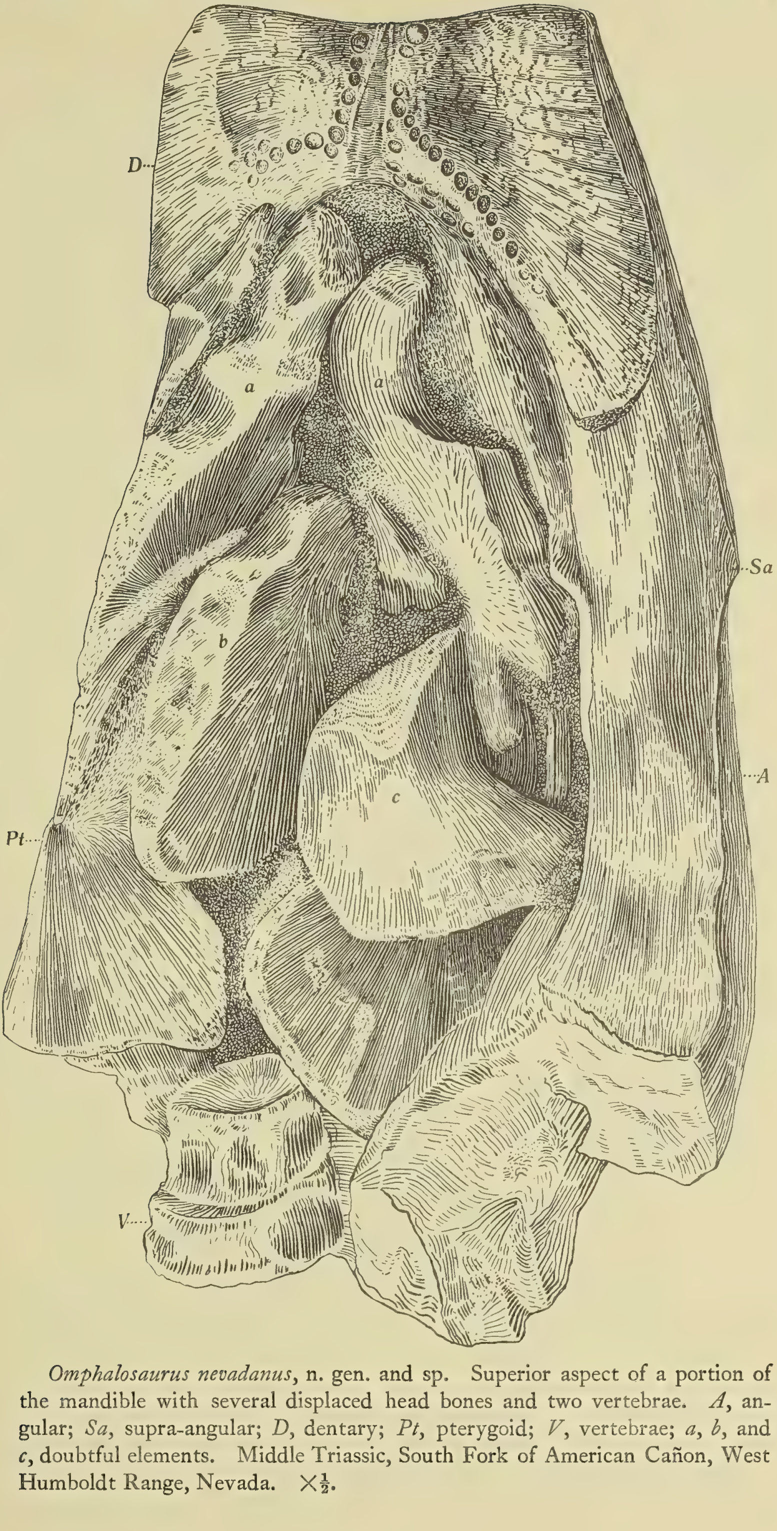
The jaw of *Placodus* possessed a large coronoid elevation. The coronoid of the Rhynchosaurs is not so well known, though such an element of considerable size seems to have been present in *Hyperodapedon minor.* The region of the coronoid is not well preserved in the *Omphalosaurus* specimen, and no definite statement as to the presence or absence of the bone can be made. In a form with crushing teeth like those seen here, such an elevation is to be expected, and it may be that the crescentic element (*c*) shown on plate 9 represents a discrete coronoid.

The structure of the mandible does not agree with that of either the Placodonts or the Rhynchosaurs. The character of the palate, so far as is known, is quite different from that in both groups. If the palatal elements are correctly interpreted, the dentition cannot be compared with that of either Placodonts or Rhynchosaurs, so far as occurrence of the teeth is concerned. The mandibular dentition is nearer to *Hyperodapedon* than to *Placodus.*

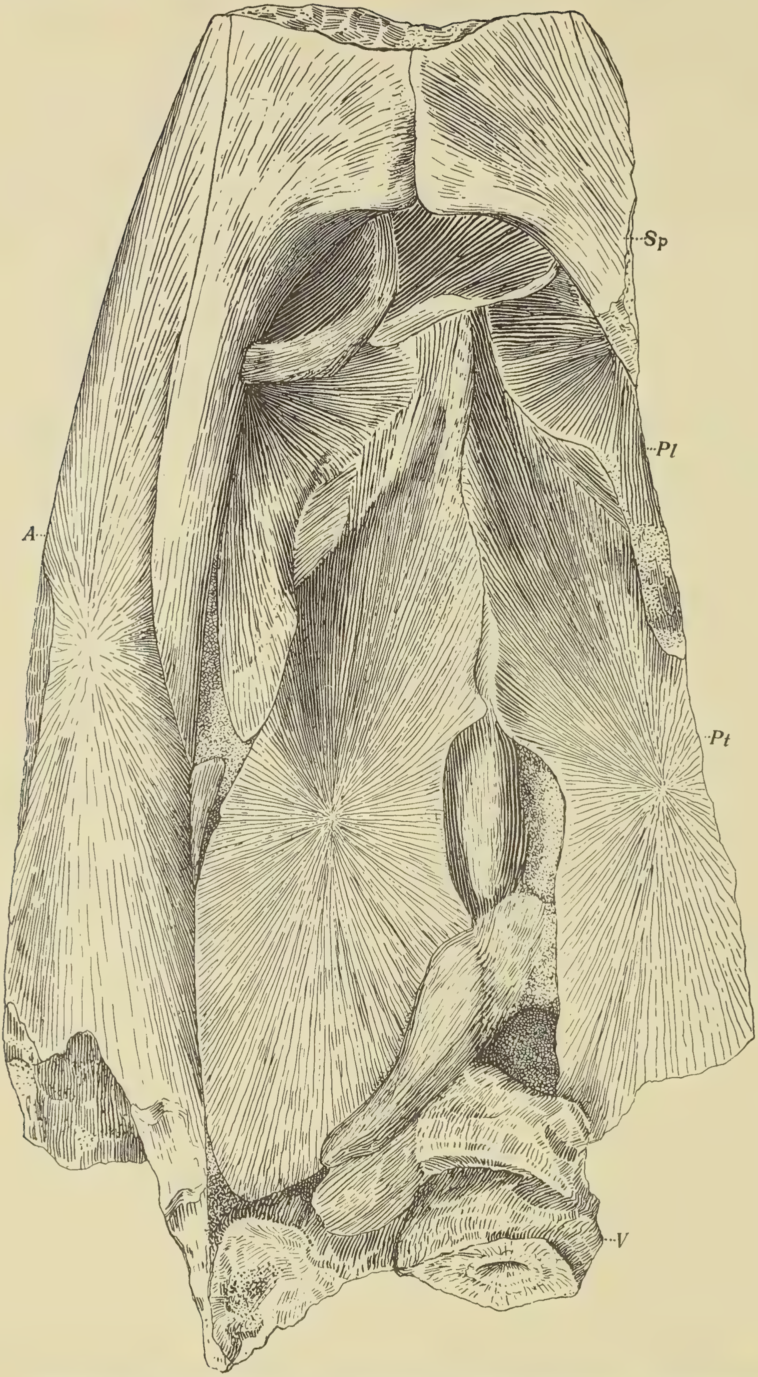
Superficially this form has the appearance of a short-headed Synapsidan. The head was evidently not greatly elongated and the cranial region presumably relatively long. The structure of the palate and of the mandible are not unlike that in the Plesiosaurs. On the other hand, certain of the characters point toward the rhynchocephalian type. The mandibular dentition is paralleled in the diaptosaurian groups, and if the two anterior elements (*a*) are vomers, they probably correspond to the large prevomers of the Diapsida.

It is quite certain that *Omphalosaurus* represents a type far enough removed from other known reptilia so that it must form a distinct family, the Omphalosauridae, but the true position of this group is not at present entirely clear. It will not improbably be found to represent an independent ordinal group among the synapsidan forms. It is hoped that the true position of this genus may be more clearly defined by the discovery of more complete specimens at the same horizon as that from which this material was obtained.

Issued December 7, 1906



Omphalosaurus nevadanus, n. gen. and sp. Superior aspect of a portion of the mandible with several displaced head bones and two vertebrae. *A*, angular; *Sa*, supra-angular; *D*, dentary; *Pt*, pterygoid; *V*, vertebrae; *a*, *b*, and *c*, doubtful elements. Middle Triassic, South Fork of American Cañon, West Humboldt Range, Nevada. ×½.



Omphalosaurus nevadanus, n. gen. and sp. Inferior view of a portion of the mandible with two vertebrae and several elements from the palatal region. *A*, angular; *Sp*, splenial; *Pt*, pterygoid; *Pl*, palatine; *V*, vertebrae. Middle Triassic, South Fork of American Cañon, West Humboldt Range, Nevada. ×½.

NOTES ON THE OSTEOLOGY OF THE THALATTOSAURIAN GENUS NECTOSAURUS

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INTRODUCTION

During the summer of 1906 an expedition from the University of California visited the exposures of the Hosselkus Limestone in the Upper Triassic of Shasta County, California, with the purpose of making a special search for material representing the recently described thalattosaurian reptiles.[1] A few scattered bones of *Nectosaurus* were found in the basal layer of the upper or massive, grey horizon of the limestone near Brushy Slope camp on the western side of Brock Mountain, but the greater part of the material representing this genus was obtained in a narrow belt of limestone near the North Fork of Squaw Creek. In the North Fork exposures numerous scattered bones including *Nectosaurus*, *Shastasaurus*, and *Thalattosaurus* were obtained in a stratum evidently representing the top of the blue, shaly lower division of the Hosselkus Limestone, or the base of the massive, grey upper division. The limestone of this horizon is composed in a large part of broken shell fragments, and the bones are almost invariably isolated, indicating that the deposit was formed in rather shallow water, where the skeletons were tossed about by the waves. At this horizon the remains are principally those of *Nectosaurus*, *Thalattosaurus* bones being comparatively rare.

SKULL AND DENTITION

There are in the collections several specimens representing the upper and lower jaws, and clearly showing the characters of the

University of California Publications, *Bulletin of the Department of Geology*, vol. 5, no. 13, pp. 217–223, pls. 17, 18, May 13, 1908.

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[1] The Thalattosauria. Merriam, J. C., Mem. Calif. Acad., Vol. 5, No. 1.

dentition. Specimen 10753 (pl. 17, fig. 1) shows nearly all of the maxillary excepting the anterior end. The posterior portion of the bone exhibits the area of contact with the lachrymal or prefrontal, and the long posterior extension which was in contact with the jugal. The teeth in this jaw are slender conical, with the crowns showing a slight lateral compression. The structure of this jaw differs considerably from that of a specimen (No. 10620) previously referred to tentatively as the maxillary of *Nectosaurus*.[2] The characters of specimen No. 10753 seem, however, to be pretty certainly those of the maxillary, and approach those of the better known *Thalattosaurus perrini*. Specimen 10620 may therefore represent one of the other dentigerous elements, though its reference is still uncertain.

A small fragment consisting of two closely united dentigerous bones (No. 10778) may represent the anterior ends of the premaxillaries or the anterior portion of the prevomers. A single perfect tooth near the anterior end of this fragment is short, thick, conical, and somewhat more acuminate than the most anterior teeth of the prevomers in *Thalattosaurus*, but much less slender than the anterior teeth of the jaws.

A number of small specimens representing the lower jaw with dentition show the teeth to be conical but apparently not as slender as in the maxillary. The crowns also show more lateral compression than was suspected in the study of the type specimen of *Nectosaurus*.

In specimen 10797 the greater part of a mandible is preserved, but the coronoid element and the dentition are unfortunately absent. The length of the jaw from the anterior end of the dentary to the middle of the cotylus is 85 mm. The height of the mandible near the middle is a little less than 13 mm.

The pterygoid is represented by several specimens which have been so weathered as to show the lateral and inferior aspects of this bone. A lateral view of No. 10770 shows the high superior wing, which is about as prominent as in *Thalattosaurus*, and is similarly sculptured. In specimen 10817 (pl. 17, fig. 3) the palatal side of a very small individual is exposed. It is not essentially different from that of the pterygoid of the type specimen of *Thalattosaurus*. The dentigerous area shows three or more longitudinal rows of distinct pits in a few of which the broken fangs of the teeth remain. The edentulous area next the base of the superior wing has about the same form as in *Thalattosaurus alexandrae*.

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[2] Merriam, J. C., Op. cit., pl. 5, fig. 6.

Another and somewhat larger pterygoid, No. 10626 (pl. 17, fig. 2) may represent *Nectosaurus* or one of the smaller species of *Thalattosaurus*. The well exposed dentigerous area shows not less than three longitudinal rows of teeth, of which one has contained at least seven teeth. The crowns are all circular in cross-section, and the two or three which are complete are slender acuminate. The bases of several of the larger teeth are distinctly seen to be anchylosed to the bone.

ARCHES AND LIMBS

The scapula of *Nectosaurus* (pl. 18, fig. 2), which has not been known before, has a form closely resembling that of *Thalattosaurus shastensis*, from which it differs mainly in its somewhat narrower distal blade.

A number of small, slender limb bones, principally representing the propodial segments of the limbs, have been found with other material referred to *Nectosaurus*. Several of these are nearly complete and show the shaft to be more slender than that of *Thalattosaurus shastensis*. The middle region of the shaft is nearly round in cross-section. The proximal end is slightly expanded. The distal extremity is considerably broadened and flattened (No. 10800, pl. 18, fig. 1). It is uncertain whether these elements represent the humerus or the femur, but in one or two cases the suggestion of foramina on the expanded distal end may indicate that these particular specimens are humeri.

In the same deposits with the larger limb elements are a number of smaller and more slender bones with less expanded ends. Though it is not possible to distinguish these certainly from those determined as propodials, it is probable that some of them represent epipodials or podials (pl. 17, figs. 4 and 5).

VERTEBRAE AND RIBS

Numerous isolated vertebrae were found in the lower portion of the upper, massive division of the Hosselkus Limestone on Brock Mountain, and in the limestones along the North Fork of Squaw

Creek. The vertebrae are always scattered, and as yet no connected series representing these forms is known. The upper arches are closely connected with the centra in nearly all cases. Only in a few instances can the line of division between them be distinctly seen, and in most instances the connection is so intimate that even the suture is almost obliterated.

The centra are all biconcave, but the terminal faces are in general not deeply cupped. In a single instance a somewhat broken centrum (No. 10806) was found which is gently concave toward the periphery of the faces, but is much more sharply excavated near the middle. The centrum is also relatively short anteroposteriorly, so that the anterior and posterior concave faces almost meet in the middle. This specimen possibly represents a middle or a distal caudal centrum of *Nectosaurus*, or may represent an ichthyosaurian genus.

The centra are about as long as high in most cases. There is evidently some variation in different regions of the column, the length being in some instances slightly greater and in others somewhat less than the height, as is indicated by the measurements below.

	Length of centrum	Height of centrum	Height of neural arch	Number of lateral apophyses
No. 10774 (dorsal?)	6 mm.	5.3	11.5	2
No. 10627 (dorsal?)	6	6.5	....	1, large
No. 10787 (dorsal?)	7.7	8.4	*a* 16.5	2 ?
No. 10779 (caudal)	5.2	5.2	13 slender	none
No. 10806	*a* 4.5	*a* 7	....	....

a, approximate.
No. 10806, possibly ichthyosaurian.

The upper arches are considerably higher than the centra. In specimen 10774 (pl. 18, fig. 6), showing a double headed articulation with the rib, the spine is considerably flattened laterally, but is not particularly broad anteroposteriorly. In specimen 10779 (pl. 18, fig. 5) with no lateral apophyses, and evidently representing the caudal region, the spine is high and very slender with almost no lateral compression. Zygapophyses are distinctly shown even in the caudal vertebra (No. 10779), where they are very prominent. In most cases the vertical element in the position of the faces of articulation seems to be much greater than the horizontal. In one specimen (No. 10787) the faces seem to have come nearer to a horizontal plane, but they are somewhat damaged and it is not possible to be absolutely certain of this determination.

The lateral apophyses in articulation with the ribs are single on some specimens and widely divided on others. On specimen No. 10627 (pl. 18, fig. 4) the large and prominent apophysis is nearly as high as the centrum, but is clearly undivided on its finely exposed articular face. A nearly obliterated line of division between the upper arch and the centrum appears to cross the apophysis some distance above the middle, as in the anterior vertebrae of *Thalattosaurus.* In specimen No. 10774 there are two distinctly separated lateral apophyses. The parapophysis is low down on the anterior margin of the centrum. The articulation of the tubercle seems to be about equally divided between the upper margin of the centrum and the base of the lower arch.

On specimen No. 10787 there is evidence of separation of a distinct inferior apophysis. The zygapophyseal faces are relatively large on this specimen and have a more nearly horizontal position than in most of the others. In this specimen the neural arch resembles considerably the anterior dorsal or cervical arch described with the type specimen of *Thalattosaurus shastensis.* If this is the case the double rib articulation might be suspected to occur in the anterior region of the vertebral column, the undivided apophyses being present on middle or posterior dorsals.

The structure of the vertebrae here referred to *Nectosaurus* is in general much like that in the genus *Thalattosaurus.* The two genera resemble each other and differ from the Ichthyosauria in the relatively slight degree of biconcavity of the centra, and in the tendency of the neural arches to fuse with the centra. A double articulation of the ribs such as is seen in some of the *Nectosaurus* specimens has not thus far been known in *Thalattosaurus.* The rib articulation is however only slightly different in the two genera. Though there is no absolute division of the lateral apophyses of the vertebrae in *Thalattosaurus*, the apophyses of the dorsal vertebrae are known to be strongly constricted. The position of the rib head with reference to the centrum and the upper arch is the same in the two genera.

A number of ribs showing well preserved articular faces have been obtained and in nearly all of these the head and tubercle are distinctly separated by a deep notch (pl. 18, fig. 3).

Conclusions

The characters of the elements of the skull and of the dentition of *Nectosaurus* are essentially of the thalattosaurian type. The nature of the attachment of the teeth is more clearly shown than it has been previously, and indicates that teeth may be set in deep, distinct pits without apparent anchylosis with the jaw, or their bases may be fused with the bone.

The limb elements obtained are all of a more elongated or more slender type than is seen in the typical *Thalattosaurus*. Those propodial elements which are well enough preserved to show the outlines of the bones are even more slender than the humerus of the small *T. shastensis*. Such material as is available seems to indicate that the epipodials and possibly the podials[3] were little more specialized than in typical shore forms. The suggestion made by the writer in a previous publication[4] that *Nectosaurus* may have been a shore dweller to a greater extent than *Thalattosaurus*, seems to be supported not only by the less distinctly specialized or adapted limbs, but also by the fact that the remains are most common in deposits containing considerable quantities of comminuted shells, which would naturally occur near the shore. The suggestion that *Nectosaurus* represents the shore-dwelling young of *Thalattosaurus* seems to be met by the fact that the dentition differs very considerably in the two forms. It should also be noted, that *Nectosaurus* is not uncommon in the deeper water deposits just above the base of the upper division of the Hosselkus Limestone, where *Thalattosaurus* has not yet been recognized.

The vertebrae and ribs agree in structure with what has previously been described for this genus and for *Thalattosaurus*, excepting that specimens have been obtained showing a distinct bicipital rib articulation in addition to those with but one articulation. The presumption is that the situation here is similar to that in some other rhynchocephalians, and in most Triassic ichthyosaurs, the anterior ribs being double-headed, while single articulation appears in the dorsal region.

Transmitted September 3, 1907
Issued May 13, 1908

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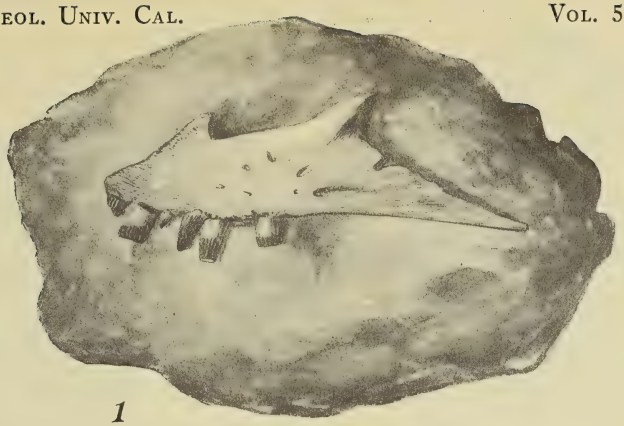
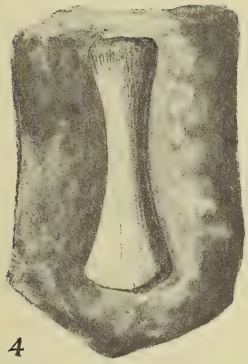
[3] The term *podials* as used here is intended to include metapodials and phalangeal elements.

[4] Merriam, J. C., Op. cit., Vol. 5, p. 23.



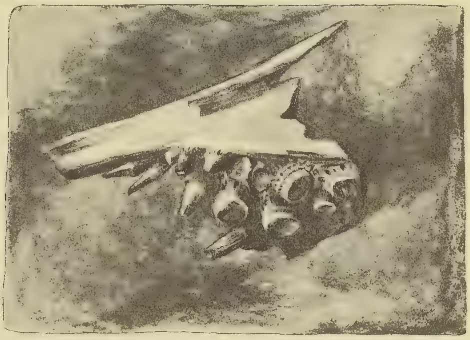
1

Left maxillary. No. 10753. × 2



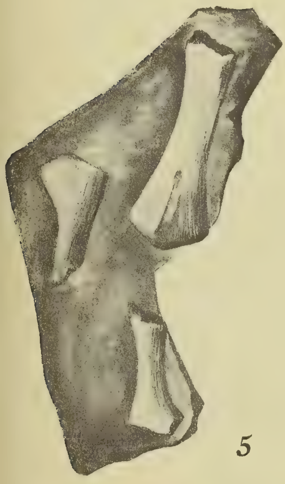
4

Epipodial? No. 10755. × 3



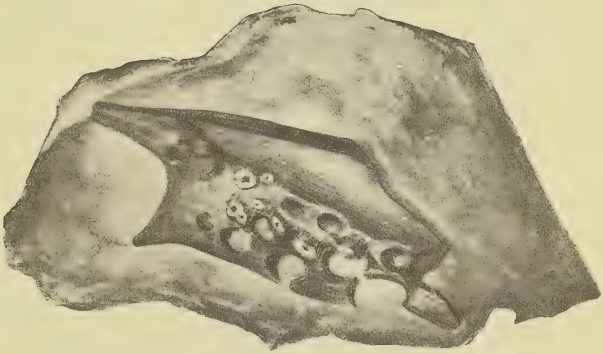
2

Pterygoid, inferior view. No. 10626. × 2



5

Epipodial? and metapodials? No. 10783. × 2

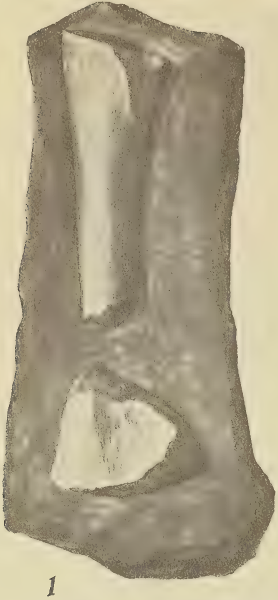


3

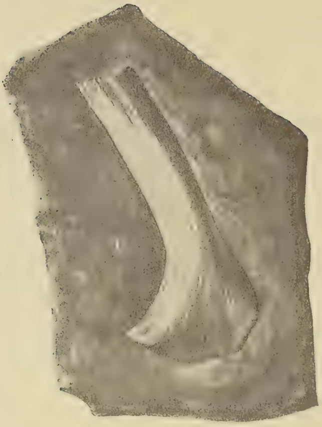
Pterygoid, inferior view. No. 10817. × 4

Nectosaurus halius Merriam

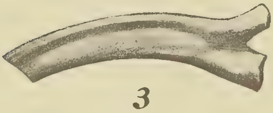
From the Upper Triassic of Shasta County, California



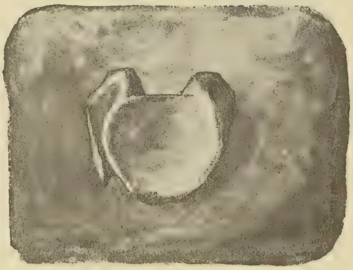
1
Propodial element. No. 10800. × 2



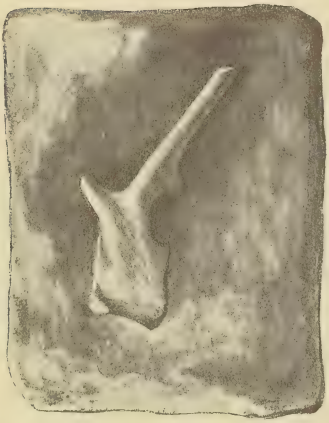
2
Scapula. No. 10803. × 2



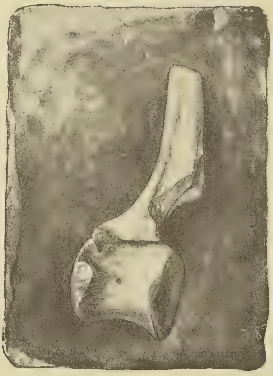
3
Rib (anterior dorsal?). No. 10758. × 2



4
Vertebra (middle or posterior dorsal?) posterior side of centrum. No. 10627. × 2



5
Anterior caudal vertebra, side view. No. 10779. × 2



6
Vertebra (dorsal?) side view. No. 10774. × 2

Nectosaurus halius Merriam
From the Upper Triassic of Shasta County, California

TRIASSIC ICHTHYOSAURIA

WITH SPECIAL REFERENCE TO THE AMERICAN FORMS

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INTRODUCTION

In a series of short papers appearing at irregular intervals since 1895, the writer has attempted to present some of the more important facts relating to the structure and occurrence of certain of the American Triassic Ichthyosauria. In the earlier stages of this work the known material was scanty and generally fragmentary, and it has not been possible in every case satisfactorily to determine the structure or the exact relationships of forms described. With a great increase in the quantity of material in the last few years, it seems advisable to bring together all available information relating to the American genera, and to consider this body of fact in relation to what is known of the earliest ichthyosaurs of other regions, as also in relation to the general problem of the evolution of this peculiar reptilian order.

Some of the questions here discussed might be considered to better advantage by workers more intimately acquainted with the extensive collections of European ichthyosaur material. The writer has, however, been emboldened to attempt generalizations bearing on the work of other investigators in this field, after consideration of the fact that the West-American collections at the present time seem to represent the largest part of the known Triassic material, and that as yet no other investigator has examined both the European and the American collections.

The investigation has been considerably delayed by the discovery of a new group of marine reptiles, the Thalattosauria, which it was necessary to understand before the true ichthyosaurian remains could be satisfactorily separated for study. Continued discoveries of ichthyosaurian material have also made it advisable to postpone publication until the new specimens could be examined. Even in its present stage the paper here presented can be considered as no more than a report of progress, as new material and additional information regarding the structure and affinities of the Triassic forms are constantly being obtained.

The material upon which the studies of the American Triassic ichthyosaurs are based includes over fifty specimens, each of which represents a considerable part of the skeleton; also a large quantity of more fragmentary material. These collections have been brought together by ten expeditions sent out by the University of California between 1901 and 1907. The material now at hand has been accumulated and made available for scientific study largely through the unflagging interest of Miss Annie M. Alexander, who has furnished the financial support for nearly all of the expeditions, and has most energetically assisted in insuring their success. The largest share of the direction of field work has been carried by Mr. E. L. Furlong, who has also prepared and mounted practically all of the specimens represented in the illustrations of Californian material in this paper.

In the initial stages of the work the writer was greatly indebted to President Benjamin Ide Wheeler of the University of California, through whose support it was made possible to extend the scale of the investigation so as to cover the broader field of the evolution of the Ichthyosauria as a whole.

In the field work carried on in connection with the investigation of the occurrence and age of the Triassic ichthyosaurs, the writer has been particularly indebted to Professor James Perrin Smith, whose knowledge of the invertebrate faunas has furnished a most valuable basis for correlation.

While working on the Ichthyosauria the writer has on several occasions visited nearly all of the American museums in which material of this group is available. The principal collections of European Jurassic ichthyosaurs have also been reviewed, and most of the described specimens from the European Triassic were examined.

In the course of this investigation the writer has been indebted to a number of the principal museums of this country and of Europe for the use of comparative material. For courteous co-operation in farthering the work of comparison, the writer is especially grateful to Dr. A. Smith Woodward and Dr. C. W. Andrews of the British Museum of Natural History; to Professor E. Fraas of the Königlichen Naturalien-Cabinet in Stuttgart; and to Dr. F. von Huene and Professor E. Koken of the Geologisch-Mineralogisches Institut in Tübingen. The use of several valuable specimens in the museum of the Polytechnikum at Zürich was kindly permitted by Professor Albert Heim; Dr. W. J. Holland kindly allowed the use of a photograph of the remarkably complete ichthyosaurian specimen in the collections of the Carnegie Museum. In working over the subject of evolution of the Ichthyosauria as a whole, the use of the collections of *Baptanodon* material in charge of Mr. W. H. Reed at the University of Wyoming, and of the types described by Mr. Gilmore at the Carnegie Museum, has been particularly helpful.

The majority of the drawings represented in the plates, also a number of the text figures, were prepared by Mrs. Grace Ballantine. The larger portion of the text figures and several of the plates, including most of the representations of vertebrae, were drawn by Mr. A. J. Heindl.

University of California
February, 1908

LITERATURE ON TRIASSIC ICHTHYOSAURIA

General references not pertaining distinctively to the literature on Triassic Ichthyosauria appear with the text as footnotes.

ARTHABER, G. VON

1896. Die Cephalopodenfauna der Reiflinger Kalke. Beitr. z. Pal. Oestr.-Ung., Bd. 10, p. 109.

BASSANI, F.

1886. Sui fossili e sull' età degli schisti bituminosi triasici di Besano. Atti della Soc. Ital. di Sc. Nat., vol. 29, p. 15.

BAUR, G.

1887. (1) On the Morphology and Origin of the Ichthyopterygia. Amer. Naturl., vol. 21, p. 839.

(2) Ueber den Ursprung der Extremitäten der Ichthyopterygia. Ber. der xx. Versam. des Oberrh. geol. Ver., Bd. 20.

CURIONI, G.

1847. Cenni sopra un nuovo saurio fossile. Giornale dell' I. R. Ist. Lomb., vol. 16.

DAMES, W.

1895. Die Ichthyopterygier der Triasformation. Sitzb. der Acad. der Wiss., Berlin, 1895, p. 1045.

BOULENGER, G. A.

1904. A new Species of Ichthyosaur. Proc. Zool. Soc. Lond., 1904, vol. 1, p. 425.

FRAAS, E.

1891. Die Ichthyosaurier der Süddeutschen Trias- und Jura-Ablagerungen, p. 37.

1896. Schwäbische Trias-Saurier. Mittheilungen aus dem Königlichen Naturalien-Cabinet zu Stuttgart, No. 5, p. 9.

HECTOR, J.

1874. On the Fossil Reptilia of New Zealand. Trans. New Zealand Inst., vol. 6, p. 355.

HUENE, F. VON

1902. Uebersicht ueber die Reptilien der Trias. Geol. u. Palae. Abh. N. F., Bd. 6, p. 10.

HULKE, I. W.

1873. Memorandum on some Fossil Vertebrate Remains collected by the Swedish Expeditions to Spitzbergen in 1864 and 1868. Bihang K. svenska Vet. Ak. Handlingar., Bd. 1, No. 9.

LEIDY, J.

1868. Notice of some Reptilian Remains from Nevada. Proc. Philad. Acad. Sc., vol. 20, p. 177.

Lydekker, R.

1889. Catalogue of the Fossil Reptilia and Amphibia in the British Museum, pt. 2, p. 113.

Merriam, J. C.

1895. On some Reptilian Remains from the Triassic of Northern California. Am. Jour. Sc., vol. 50, p. 55. July.

1902. (1) Triassic Reptilia from Northern California. Science n. s., vol. 15, p. 411. Mar. 14.

(2) Triassic Ichthyopterygia from California and Nevada. Univ. Calif. Publ. Geol., vol. 3, no. 4. June.

(3) Primitive Characters of the Triassic Ichthyosaurs. Bull. Geol. Soc. Am., vol. 14, p. 536.

1903. (1) New Ichthyosauria from the Upper Triassic of California. Univ. Calif. Publ. Geol., vol. 3, no. 12. May.

(2) Recent Literature on Triassic Ichthyosaurs. Science n. s., vol. 18, p. 311. Sept. 4.

1904. Types of Limb-structure in Triassic Ichthyosaurs. Science n. s., vol. 19, p. 218. Feb. 5.

1905. (1) Types of Limb-structure in the Triassic Ichthyosauria. Am. Jour. Sc., vol. 19, p. 23. January.

(2) A Primitive Ichthyosaurian Limb from the Middle Triassic of Nevada. Univ. Calif. Publ. Geol., vol. 4, no. 2. March.

Meyer, H. von

1847. Mittheilung an Professor Bronn gerichtet. N. Jahrb. f. Min., 1847, pp. 190 and 191.

1855. Zur Fauna der Vorwelt. Die Saurier des Muschelkalkes, p. 129 and Taf. 57, Fig. 3a, 3b, and 3c.

1856. Mittheilungen an Professor Bronn gerichtet. N. Jahrb. f. Min., 1856, pp. 824 and 825.

Phillips, J.

1871. Geology of Oxford, pp. 101 and 106.

Quenstedt, F. A.

1852. Handbuch der Petrefactenkunde, p. 129, Taf. 6, Fig. 7–10.

Repossi, E.

1902. Mixosauro degli strati triasici di Besano in Lombardia. Atti della Soc. Ital. di Sc. Nat., vol. 41, p. 3.

Sauvage, H. E.

1876. Note sur les Débris d'Ichthyosaure des Couches Rhétiennes de Saône-et-Loire. Ann. Sc. Géol., t. 7, art. 6.

1883. Recherches sur les Reptiles Trouvés dans l'Etage Rhétien des Environs d'Autun. Ann. Sc. Géol., t. 14, art. 3.

1903. Note sur les Reptiles de l'Etage Rhétien des Environs d'Autun. Bull. d. l. Soc. d'Hist. Nat. d'Autun, 1903, p. 309.

Yakowlew, N.

1902. (1) Neue Funde von Trias-Saurien auf Spitzbergen. Verh. d. Kais. Russ. Min. Ges., Bd. 40, p. 179.

(2) Einige Bemerkungen ueber Triassische Ichthyosaurier. Verh. d. Kais. Russ. Min. Ges., Bd. 40, Lief. 2.

HISTORICAL REVIEW OF LITERATURE

The earliest reported discoveries of Triassic ichthyosaurian remains were made known by Herman von Meyer and by G. Curioni in 1847. The material available for von Meyer's studies consisted of a few teeth and vertebrae, and an imperfect sketch of a saurian found at Reiflingen in Steyermark in 1843 by Professor Pranger. Von Meyer knew also of a vertebra from Ettersberg near Weimar. These specimens were mentioned by von Meyer principally because of their occurrence in beds considerably older than those in which the typical ichthyosaurs were known. Nothing particularly characteristic was noted in their structure, and the Reiflingen specimen was compared with Cuvier's figured specimens described as *Ichthyosaurus platyodon.*

In the same year in which von Meyer announced his discovery of Triassic ichthyosaurian remains, G. Curioni gave notice of the occurrence, in the bituminous shales of Besano, of a form which he referred to *Ichthyosaurus communis.*

In 1852 fragmentary specimens from the Wellendolomit of the Black Forest, including a vertebra, some paddle bones, and a jaw fragment with teeth, were described under the name of *Ichthyosaurus atavus* by Quenstedt.

In 1855 von Meyer described from the Muschelkalk of Ober-Schlesien a vertebra which resembled a dorsal of an ichthyosaurian. In connection with the description of this specimen reference was made to a somewhat similar vertebra described (Palaeontographica, Bd. 1, p. 253, Taf. 29, fig. 55) from Larishof in Ober-Schlesien. This vertebra seemed to show a natural perforation of the centrum. Accompanying it there is figured a vertebra with a central perforation of the centrum, and with a broad unexcavated margin surrounding the deeply concave middle region of the articular face. In 1856 von Meyer gave a brief description of two vertebrae from the Koessner beds of Schleimser Joch in Achenthal and noted their resemblance to *Ichthyosaurus tenuirostris.* Up to this time no evidence had been obtained which tended to show that the Triassic forms were materially different from the typical Jurassic ichthyosaurs.

In 1868, and before the true nature of any European Triassic ichthyosaurian had been made clear, Leidy described the first known specimens from America. Though the material at Leidy's command was very fragmentary, the distinguishing characters of the type they represent could have been made out had some of the enveloping limestone been removed. The characters referred to in the original description were principally those of ordinal value.

In 1873 Hulke described the first ichthyosaurian remains known from Spitzbergen, referring them to *Ichthyosaurus*, of which two species, *I. polaris* and *I. nordenskiöldii* were described. It is apparent from Hulke's description that the single-headed character of the ribs in the dorsal region was recognized, but no special value was assigned to it. The same material was worked over again by Dames in 1895, and assigned to the genus *Mixosaurus*. Curiously enough, Dames failed to accept the statement that single-headed ribs of this character occurred in *Shastasaurus*, and assumed that the ribs must be double-headed as in *Mixosaurus*, of which he appears to have had little available information.

In 1876 Sauvage described from the Rhaetic of Saône-et-Loire in France two types of vertebrae designated as *Ichthyosaurus rheticus* and *I. carinatus*. In 1883 these species were figured and more fully described by Sauvage, there being, however, only fragmentary material available. In the same publication, Sauvage described under the name *Rachitrema pellati* a form represented by a vertebral arch, a scapula, and several fragmentary arch and limb bones. *Rachitrema* was referred by Sauvage to the Dinosauria, but was later referred to the Ichthyosauria.

The description of a Triassic ichthyosaurian species, *Ichthyosaurus cornalianus*, from the bituminous shales of Besano in northern Italy, by Bassani in 1886, marked the beginning of the first studies of the forms in which sufficient material was available for satisfactory investigation of the skeletal characters.

In 1887, shortly after the description of the Besano specimen by Bassani, Baur (1887, 2) published his brief but important note on the structure of the limbs of the Italian specimens. It was then for the first time clearly shown that the ichthyosaurian limb in the Triassic stage of development was much farther away from the fish type than were the limbs of the succeeding Jurassic forms. The form of the limb elements was somewhat exaggerated in Baur's figures, and his suggestion concerning the origin of the outer element in the mesopodial region in the limb of *Baptanodon* is perhaps overstated, but his fundamental theory was correct. Baur set aside the Triassic ichthyosaurs with elongated epipodial elements separated by a cleft as a distinct genus, *Mixosaurus*, and divided the Ichthyosauria into three families: the MIXOSAURIDAE with elongated and separated epipodial bones and differentiated dentition; the ICHTHYOSAURIDAE with short epipodials which touch each other, and numerous teeth of nearly uniform shape; the BAPTANODONTIDAE with three epipodial elements, and no teeth.

In 1891 Fraas described and figured several jaw fragments, a humerus, and a number of vertebrae from the Wellendolomit of South Germany, referring all of these specimens to *Mixosaurus atavus* (Quenstedt). Attention was called to the contrast between the depressed crowns of the posterior teeth and the slender conical crowns of those farther forward in the jaw. The insertion of the teeth was also found to differ from that in *Ichthyosaurus*, inasmuch as the fangs were set into the jaw instead of resting in an open groove. The separate zygapophysial facets of the vertebrae were shown to be placed in intersecting planes, in contrast to the facets in *Ichthyosaurus*, where they are brought into the same plane and united medially. The vertebral centra were found to be deeply biconcave, and to be perforated by the chorda dorsalis in the caudal region. The specimens referred to *M. atavus* were divided into two varieties, *major* and *minor*.

In 1895 Merriam described the genus *Shastasaurus* from the Upper Triassic of northern California. The type specimen consisting of eight connected vertebrae, an arch bone and several ribs was distinguished from other genera by the thickened neural spines of the vertebrae, the single-headed dorsal ribs and the peculiar form of the coracoid. The element held to be a coracoid by the writer, and by all others who have expressed an opinion as to its character, was found later to be a pubis quite different from any known ichthyosaurian element. The vertebrae and ribs were from the posterior dorsal region.

In 1902 the description of the Californian Triassic ichthyosaurs was continued by Merriam with better material available. From these specimens it was possible to determine the principal characters of the skeleton, excepting the anterior portion of the skull and the phalangeal region of the paddles. The material was also found to represent several specific forms, one of which, *Shastasaurus perrini*, was later removed as a distinct genus, *Delphinosaurus*. In this publication Leidy's types of the Middle Triassic ichthyosaurs of Nevada were redescribed, and attention was called to their similarity to the shastasaurian forms. A collection of ichthyosaurian material obtained from the Middle Triassic of Nevada by the University of California before this paper appeared was referred to as apparently representing *Cymbospondylus petrinus* of Leidy. This material was stated to show a number of peculiar characters not recognized in specimens previously examined.

In November 1902 a fully illustrated paper by Repossi furnished the first definite information regarding the general skeletal structure of *Mixosaurus*. In Repossi's figures it was shown that *Mixosaurus* possessed many primitive characters that had not been recognized before. It appeared also to be much more closely related to the American Triassic forms than had been supposed. Also in 1902, there appeared Yakowlew's publication on a new find of ichthyosaurian remains from Spitzbergen, in which the large Spitzbergen form (*Ichthyosaurus polaris* of Hulke) was shown to have single-headed dorsal ribs, and was referred to *Shastasaurus*.

In von Huene's valuable work on the Triassic Reptilia, issued in 1902, there was given a brief review of the literature on the Ichthyosauria. Von Huene also presented the first figures of the interclavicle of a Triassic form, showing an interesting evolution from a deltoid Triassic type to the T-shaped element of the Jurassic ichthyosaurs. New material from the vertebral column was also described and figured.

In 1903 new material from California made possible the description of a complete anterior limb of an American Triassic ichthyosaurian (Merriam, 1903, 1). In this genus (*Leptocheirus* Merriam—*Merriamia* Boulenger) instead of the primitive pentadactyl structure of the mixosaurian limb only three complete digits were represented. In another form, *Toretocnemus*, the hind limb was fully as large as the anterior one, but there were apparently only three digits and a very rudimentary fourth in the podial region. The pelvis of *Toretocnemus* was plate-like, and the pubis perforated by an obturator foramen. The middle dorsal vertebrae, unlike those of *Shastasaurus* and *Delphinosaurus*, supported double-headed ribs.

The first description of other than fragmentary remains from the Middle Triassic of America appeared in 1895 in the discussion of a finely preserved pectoral arch with the propodial and epipodial limb segments (Merriam, 1905, 2). The shoulder girdle of this form differed from that of any other known ichthyosaur, and the limb elements appeared to be the most primitive then known in the Ichthyosauria.

Geologic and Geographic Occurrence

The geographic range of the Triassic ichthyosaurs is remarkably wide almost as far back as we can trace the group. Even from the Middle Triassic, remains are known from both Europe and western North America. From the Upper Triassic they are known from these regions, and possibly from others also.

Europe.—The oldest known remains of Ichthyosauria are those from the lower portion of the Muschelkalk of Germany and Switzerland. Fraas (1891, p. 37) states that the localities in the Swabian Muschelkalk at which specimens have been found represent a very constant horizon in the Wellendolomit. Unfortunately the material obtained consists only of isolated vertebrae, jaw fragments, or other separated parts of the skeleton. As yet no complete skeletons have been discovered.

A small amount of material from the lower Muschelkalk of southwest Germany and northern Switzerland is preserved in the collections of the Königlichen Naturalien-Cabinet, and in that of the Technische Hochschule in Stuttgart, in the Geologisch-Mineralogisches Institut in Tübingen, and in the Polytechnikum in Zürich. A few specimens of ichthyosaurian vertebrae from the lower Muschelkalk in North Germany are preserved in the geological museum of Halle a. S. Of the Swabian localities where material has been found in the Wellenkalk of the lower Muschelkalk, Fraas has mentioned Rohrdorf, Calw, Aach, and Niederschach. The vertebrae at Zürich came from the Wellendolomit of Laufenberg in Canton Aargau and from Obereggingen. Material from the Wellenkalk of Querfurt north of the Harz is in the museum at Halle a. S.

From the middle of Muschelkalk of Freyburg a. U. ichthyosaur-like vertebrae have been obtained.

The upper Muschelkalk of Bayreuth has furnished several valuable specimens, including vertebrae and elements from both pectoral and pelvic arches. Descriptions of some of these specimens will probably appear in the near future. Also from the upper Muschelkalk are several vertebrae of ichthyosaurians from Grossreifling in Steiermark. From this locality there was also obtained in 1843 a very large skull with numerous vertebrae and other elements of the skeleton. This specimen was destroyed by fire in the museum of Admont in 1863. No careful study of it was made by a specialist in vertebrate palaeontology. At the present time there is some uncertainty as to its true character. H. von Meyer (1847, pp. 190 and 191) described it from a sketch, and from information furnished by others, and compared it with *Ichthyosaurus platyodon*. A copy of an old sketch reproduced by von Arthaber (1896, p. 14) does not show any characters which indicate other than ichthyosaurian affinities. Other upper Muschelkalk remains, now in the mineralogical museum of Jena, are known from beds near Weimar.

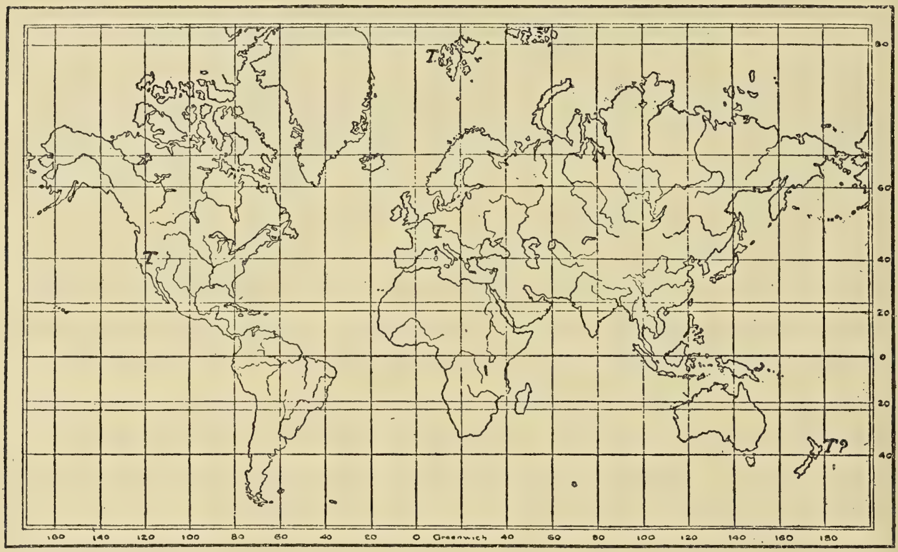
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Fig. 1. Outline map of the world, on which the regions where Triassic ichthyosaurian remains have been found are marked with the letter *T*.

Not until the Upper Triassic is reached in Europe do we find ichthyosaurian remains which give more than suggestions as to the true nature of the forms in the Triassic which they represent. The most abundant and important Triassic ichthyosaur material known in Europe is that from the bituminous shales of Besano in the vicinity of lake Lugano in northern Italy. This horizon has been stated to be the equivalent of the Raibl.[1] The Raibl is referred to the Upper Trias,[2] but more recent investigations have seemed to show that this horizon may be somewhat older. The material comprises a number of finely preserved skeletons exhibiting practically all parts of the skeletal structure. In addition there are a number of isolated parts of skeletons which help to interpret some of the larger specimens. On this material Bassani (1886) based *Ichthyosaurus cornalianus*, which later became the type of Baur's (1887) genus *Mixosaurus*.

From the Rhaetic portion of the Upper Trias Sauvage (1876) has described fragmentary remains apparently representing two species of primitive ichthyosaurs, *Ichthyosaurus rheticus* and *I.* (*?*) *carinatus*. Vertebrae are also known from the Swabian Bonebed (von Huene, 1902) and from the Koessner bed of Achnerthal (von Meyer, 1856). From Rhaetic beds near Bristol, England, a number of ichthyosaurian remains are also reported (Phillips, 1871).

Spitzbergen.—The occurrence of ichthyosaurian remains in the Triassic Spitzbergen was made known by Hulke in 1873 in a short paper on some fragmentary material obtained by a Nordenskiöld expedition in 1864 and 1868. The remains were referred to *Ichthyosaurus* by Hulke. Later observation by Merriam (1902) and Yakowlew (1902) have shown that Hulke's specimens were related to *Shastasaurus*. Dames (1895) supposed them to belong in *Mixosaurus*, but was unfortunately not well acquainted with the structure of that form, and also misinterpreted the first description of *Shastasaurus*. The original material of Hulke's species was lost after being studied by Dames in 1895.

A good fragment of a vertebra, obtained by the Russian-Swedish expedition in 1899–1901, was described by Yakowlew (1902) and referred to *Shastasaurus*.

New Zealand.—In 1874 Hector described from New Zealand an ichthyosaurian vertebra obtained in a micaceous sandstone in the

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[1] Bassani, F., Atti Soc. Ital. Sc. Nat., vol. 29. Milano, 1886.

[2] See table on p. 224.

Rangitata district of the province of Canterbury. The formation in which it occurred was said to be identical with other strata considered to be Triassic.

America.—The occurrences of Triassic ichthyosaurians in America have thus far been limited to exposures of the marine Trias in California and Nevada (fig. 2). As in Europe, remains are known from both the Upper and Middle Triassic, the oldest known specimens coming from the Middle Trias. The Upper, Middle and Lower Trias are all three represented in California and probably in Nevada also, but the conditions favoring the preservation of fossils are not similar in corresponding horizons of the two regions. For this reason it has chanced that ichthyosaurs are known as yet only from the middle division of the Trias in Nevada and from the upper division in California. In the fossiliferous marine Lower Triassic limestones of California and Idaho no remains of reptiles have yet been obtained, though marine fishes are common in the Lower Triassic of Idaho.

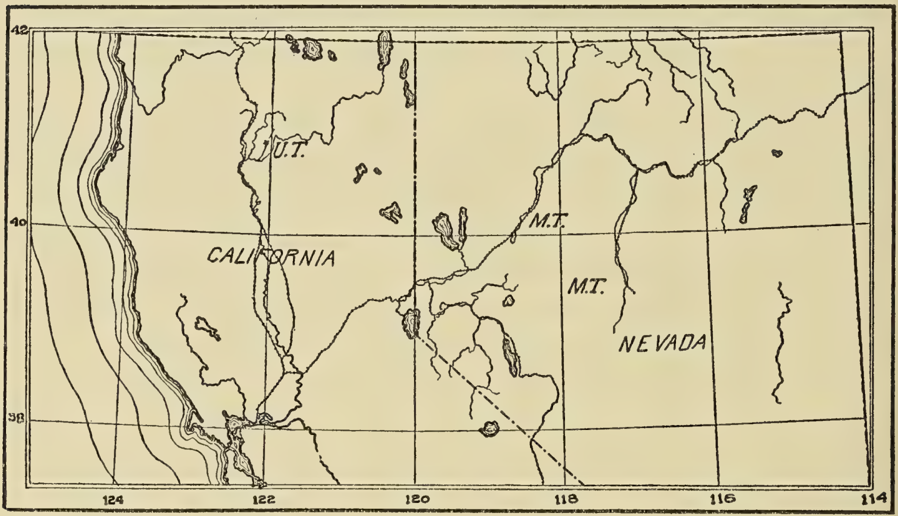

Fig. 2. Sketch map of northern California and northwestern Nevada, giving occurrence of Triassic formations in which ichthyosaurians have been obtained; *UT*, Upper Triassic; *MT*, Middle Triassic.

The geological correlation of the marine Triassic of the Pacific Coast region of America has been made the subject of careful investigation by Professor James Perrin Smith, from whose work on the stratigraphy of the West American marine Trias[3] the table on the following page has been extracted.

The *Upper Triassic* beds containing ichthyosaurian remains in California are largely exposed in Shasta County between the west side of Pit river and Squaw creek.[4] Large exposures form the imposing gray cliffs and peaks along the top of the prominent series of points known as Brock mountain (pl. 1, fig. 2). The outcrops also cross Pit river to the south, and extend to the north in rather narrow exposures beyond the headwaters of the North Fork of Squaw creek. The formation consists principally of the phase known as the Hosselkus Limestone. It is rather sharply divided lithologically into an upper and a lower portion (pl. 1, figs. 2 and 3). The upper part consists of very massive, gray limestones. The lower beds are composed of dark gray or black, somewhat shaly limestones, and bands of calcareous black shales. Below the lower division are the black Pit Shales of the Middle Trias.

The Hosselkus Limestone contains in its fauna a large number of invertebrate forms, of which the greater number of the species are Cephalopoda. In addition to the Ichthyosauria, the vertebrates are represented by the thalattosaurian reptiles, and by a few fishes.[5] A list of the characteristic species would include the following:

Tropites subbullatus Hauer
Tropites dilleri Smith
Discotropites sandlingensis Hauer
Sagenites herbichi Mojsisovics
Juvavites subintermittens Hyatt and Smith
Polycyclus henseli Oppel
Arpadites gabbi Hyatt and Smith
Californites merriami Hyatt and Smith
Clionites compressus Hyatt and Smith
Sandlingites andersoni Hyatt and Smith
Sirenites lawsoni Hyatt and Smith
Trachyceras lecontei Hyatt and Smith
Hauerites ashleyi Hyatt and Smith
Arcestes pacificus Hyatt and Smith
Cosmonautilus dilleri Hyatt and Smith
Orthoceras shastense Hyatt and Smith
Halobia superba Mojsisovics
Terebratula, sp. indet.
Rhynchonella, sp. indet.
Myophoria, sp. indet.
Thalattosaurus alexandrae Merriam
Thalattosaurus perrini Merriam
Nectosaurus halius Merriam
Hybodus shastensis Wemple
Acrodus wempliae Jordan

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[3] Smith, Jas. Perrin, Festschrift zum siebzigsten Geburtstage von Adolf v. Koenen, 1907.

[4] Diller, J. S., U. S. Geol. Surv., Redding folio.

[5] Merriam, J. C., The Thalattosauria, Mem. Calif. Acad. Sci., vol. 5, no. 1.

Wemple, Miss E. M., New Cestraciont Teeth from the West-American Trias, Univ. Calif. Publ. Geol., vol. 5, no. 4.

Jordan, D. S., The Fossil Fishes of California, Univ. Calif. Publ. Geol., vol. 5, no. 7.

Ichthyosaurian remains have been found in nearly all horizons of the Hosselkus Limestone. They are nowhere very abundant, several years work having brought in only about twenty good specimens. They are most numerous in the *Tropites subbullatus* and *Juvavites* horizons near the top of the lower division. In the lower, more shaly beds little material has been found, but the specimens occurring there were in good state of preservation and the elements were not badly scattered. In a well marked bed a short distance

INTERREGIONAL CORRELATION OF THE TRIAS (ADAPTED FROM JAS. PERRIN SMITH)

	Mediterranean region			Arctic-Pacific region			American region						
	German	Alpine					California		Nevada		Idaho		Brit. Col.
	Rhaet												
UPPER TRIAS	Keuper	Noric limestone of Hallstatt	*Pseudomonotis ochotica* in the Crimea	*Pseudomonotis ochotica* slates of northern Sibera, Japan and Indian Ocean				*Pseudomonotis subcircularis* slates with *Rhabdoceras* and *Halorites*	*Pseudomonotis* slates with *Rhabdoceras* and *Placites*				*Pseudomonotis* slates
							Hosselkus limestone	*Spiriferina* beds	Star Peak limestones without characteristic fossils				
								Juvavites beds					
		Sandling beds with *Tropites subbullatus*						Beds with *Tropites subbullatus*					*Dawsonites* beds
		Raibl beds with *Trachyceras aonides*		*Dawsonites* slates of Bear Island				*Halobia superba* beds					
		Cassian beds with *Trachyceras Aon*						Slates with *Halobia* conf. *rugosa*					
		Wengen beds with *Trachyceras Archelaus*					Pit Formation	Slates and tuffs without determinable fossils					*Daonella* beds
MIDDLE TRIAS	Upper Muschelkalk	Buchenstein beds with *Trachyceras Reitzii*		Ceratite slates of Japan with *Anolcites* and *Danubites*					*Daonella* limestones in western Humboldt Range	*Daonella dubia* beds with *Ceratites trinodosus*			
	Middle Muschelkalk	Reifling limestone	Limestones of Han Bulog, Bakony and the Schrey Alps with *Ceratites trinodosus*	Beds of Ussuri Bay in eastern Siberia with *Monophyllites sichoticas*	Mengilaeh beds?	*Daonella* limestones of Spitzbergen		Clay- and silicious slates with *Anolcites* conf. *Whitneyi* and *Ceratites* conf. *humboldtensis*					
	Lower Muschelkalk with *Hungarites Strombecki*	*Ceratites binodosus* beds in the South Alps				*Posidonomya* limestones of Spitzbergen					Aspen beds		
		Beds at Gulf of Ismid in Asia Minor					Ceratite limestones of Inyo Range	Black limestones with *Parapopanoceras*, *Xenodiscus*, *Acrochordiceras*, and *Hungarites*					
LOWER TRIAS	Buntsandstein	Werfen beds	Campil beds with *Tirolites cassianus*	Olenek beds of northern Siberia				Calcareous slates without fossils				*Columbites* beds	
				Proptychites beds of Ussuri Bay in northern Siberia				*Meekoceras* beds of Inyo County, California with *Meekoceras gracilitatis*, *Ussuria*, *Pseudosageceras*, *Inyoites*, *Owenites*, *Nannites*				*Tirolites* beds	
			Seis beds with *Pseudomonotis Clarai*									*Meekoceras* beds	

below the top of the lower division many loose vertebrae and other skeletal elements have been found associated with comminuted shells, evidently representing somewhat shallower water than the rest of the deposits. In the massive, gray beds of the upper Hosselkus Limestone the remains are usually fragmentary and scattered. Some large specimens showing connected parts of skeletons have, however, been found there.

As yet the genera *Delphinosaurus*, *Toretocnemus* and *Merriamia* are known only from the beds some distance below the top of the lower division; *Shastasaurus* occurs in both lower and upper divisions, but is represented in the upper beds principally by the gigantic *S. careyi*.

In the Upper Triassic specimens, excepting in a very few instances, the limestone matrix is cemented to the bones, making the work of preparation more than ordinarily difficult. In the case of small specimens, etching with hydrochloric acid has been found advantageous; the blue tint of the mineral vivianite appears in the bones, making their outlines comparatively distinct.

The *Middle Triassic* ichthyosaurs of the Pacific Coast region have thus far been known only from the limestones of the West Humboldt and New Pass ranges of Western and Central Nevada (fig. 2). Search has been made in the Middle Triassic shales of California but without any definite results.

The most important occurrences are those in the exposures along the eastern side of the West Humboldt Range. Wherever the limestones are exposed bones may occur. The most important finds have been made at Cottonwood, Buena Vista, Straight, Indian, American, and Fisher cañons. In the south fork of American Cañon on the two points known as Saurian Hill and Fossil Hill (pl. 1, fig. 1) skeletons were particularly numerous and well preserved.

The horizon at which the ichthyosaurs of the West Humboldt Range occur is apparently a constant one, representing the middle portion of the Middle Triassic. The associated invertebrate fauna as described by James Perrin Smith includes with others the following characteristic forms:

Daonella dubia Gabb
Orthoceras dubium Gabb
Atractites conf. *crassirostris* Hauer
Ceratites trinodosus Mojsisovics
Anolcites americanus Mojsisovics
Acrochordiceras hyatti Meek

Gymnites aff. *bosnensis* Hauer
Ptychites meeki Hyatt and Smith
Celtites halli Mojsisovics
Monophyllites billingsianus Gabb
Sageceras gabbi Mojsisovics
Eutomoceras dunni Smith
Joannites gabbi Meek
Beyrichites rotelliformis Meek

This fauna is that of the characteristic *Ceratites trinodosus* horizon, and *C. trinodosus* is a common species.

In addition to the Ichthyosauria there have been found in these beds a few fishes, and some reptilian forms which are as yet only imperfectly known. The following are the described forms.[6]

Acrodus alexandrae Wemple
Acrodus oredontus Wemple
Hybodus nevadensis Wemple
Omphalosaurus nevadanus Merriam

The skeletons are in general better preserved in the Middle Triassic beds of Nevada than in the later limestones of northern California, and are more easily freed from the matrix. The limestone is often slightly shaly, and is frequently separated from the bone by a thin film of argillaceous material heavily impregnated with iron oxide. In a few localities of comparatively small area the ichthyosaur skeletons are very numerous. The writer is not aware of any locality in other formations at which remains of ichthyosaurs are more abundant.

At American Cañon, where the most extensive work has been carried on, the beds have fortunately been repeated twice by faults, giving a large exposure of the most fossiliferous strata. In this region, between thirty and forty good specimens were obtained on Saurian Hill, and from the same bed repeated on Fossil Hill farther to the east.

In many cases there seems to be a concretionary formation about the skeletons. This is most distinctly shown in the case of the skull, which may be enclosed in a rounded nodular mass. This structure is noticeable also in following the vertebral column, the layer containing the vertebrae often pinching out on both sides of the skeleton. Unfortunately the ends of the limbs seem often to have extended beyond the nodular envelope, and are not to be found in the rock immediately outside of it.

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[6] Wemple, Miss E. M., New Cestraciont Teeth from the West-American Trias. Univ. Calif. Publ. Geol., vol. 5, no. 4.

Merriam, J. C., Preliminary Note on a New Marine Reptile from the Middle Triassic of Nevada. Univ. Calif. Publ. Geol., vol. 5, no. 5.

The Triassic beds in the New Pass Range are of nearly the same age as those in the West Humboldt Range. The exposures are not as extensive as in the West Humboldt Range and the beds are hardly as rich in fossils.

The following are, according to Professor Smith, the most characteristic species of this locality:

Celtites neumayri Mojsisovics
Ceratites (*Paraceratites*) *trinodosus* Mojsisovics
Trachyceras americanum Meek
Ceucoceras bonae-vistae Hyatt and Smith
Arcestes gabbi Meek
Gymnotoceras blakei Gabb

In the New Pass Range thirty miles west of Austin and three miles west of the New Pass mine several parts of ichthyosaurian skeletons were obtained. The first specimen of a Middle Triassic ichthyosaurian to be described from America was found at this locality (Leidy, 1868).

The Middle Triassic limestones are represented at other points in Nevada, and will probably be found to have ichthyosaurian remains more or less abundantly represented in them wherever they occur.

Though it is probable that the Ichthyosauria had become marine forms as early as Lower Triassic time, no one has yet succeeded in obtaining in America any material representing the group from beds lower than the middle division of the Trias. The marine Lower Trias of eastern California and particularly of southeastern Idaho is very rich in fossils, including cephalopods, with which ichthyosaurs are elsewhere associated; but as yet no bones have been obtained which can be referred to reptilian orders. Bones of crossopterygian fishes are fairly common in these beds[7] in association with cephalopods.

The distribution of the Triassic ichthyosaurs, ranging as it does from Europe and Spitzbergen to western North America and possibly to New Zealand, apparently indicates that these forms were in existence as a marine type for a considerable period even antecedent to Middle Triassic time. As early as the Middle Triassic, forms showing a considerable degree of specialization were present in western Europe and in western North America. Even though a wide range of open sea between these two provinces be presumed to have existed, such a wide distribution as is seen here could not have been accomplished in less than a considerable part of an epoch.

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[7] Goddard, M., Fish Remains from the Marine Lower Triassic of Aspen Ridge, Idaho, Univ. Calif. Publ. Geol., vol. 5, no. 8. Also, Evans, H. M., A New Cestraciont Spine from the Lower Triassic of Idaho, Univ. Calif. Publ. Geol., vol. 3, no. 18.

The wide distribution of the Ichthyosauria in Middle Triassic time with the absence of any known remains from the Lower Triassic makes it difficult to determine even approximately the place of origin of the group.

General Skeletal Structure of the Triassic Ichthyosaurs

Though there is much variation in the structure of the ichthyosaurians known from the Triassic, and there is good reason for considering them as divisible into several natural subgroups, it is also true that they are evidently a unit or a distinct group, the greater part of the evolution or differentiation of which from the primitive type has taken place in Triassic time. It has therefore seemed important for purposes of comparison to consider the general structure of all the known forms together. In another portion of this paper the characteristics of the subgroups are discussed separately.

Skull

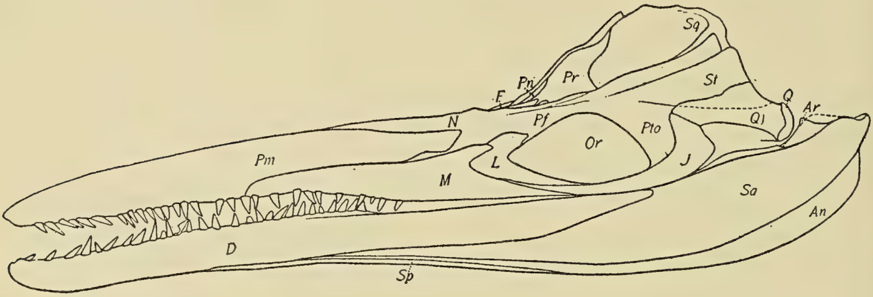
In all Ichthyosauria, whether from the Triassic or from later periods, there is a remarkable similarity of general characters in the structure of the skull. Though considerable differences appear in a comparison of all the known forms, particularly in contrasting the oldest genera with the most recent ones, these differences consist in the main of variations in the proportions of parts, and almost no radical changes of characters such as may occur in other parts of the skeleton are found here. The modifications or variations which present themselves during the known history of the group are in the main closely related to variations in the length of the elements of the facial region, or to change in the size of the orbits. The varying characters seem to be almost entirely of the adaptive type, and indicate a close relationship between the evolutionary changes in the group and the greatest needs of the animal under the particular conditions obtaining in its habitat.

The structure of the skull is well shown in the Italian mixosaurs, but as yet no detailed study of this portion of the skeleton has been carried out in these specimens, and only the most general observations can be made on the figures available. Of the other material obtained in Europe, only a few fragments are known. Of the American Upper Triassic fauna the skulls of *Shastasaurus*, *Merriamia* and *Delphinosaurus* are known in part, but without satisfactorily showing the features which ordinarily give most definite expression to variation tendencies. Of the American Middle Triassic *Cymbospondylus* practically the entire skull structure is well shown in several excellent specimens (pls. 2 to 6). As *Cymbospondylus* is the only Triassic genus of which the skull is well known, its description is made the basis for the following discussion of the skull of the Triassic Ichthyosauria in general.

Although it represents one of the most ancient known ichthyosaurs and is relatively primitive in many respects, the skull of *Cymbospondylus* is still typically ichthyosaurian. While its structure, like that of the limbs, approximates that of shore types more closely than do the corresponding features in the Jurassic ichthyosaurs, it is as a whole surprisingly specialized, and is evidently the product of an ancestry which had expressed this special type of aquatic adaptation for a long period. Like the typical Jurassic genera, the facial region is relatively long and slender, the premaxillaries and nasals are very largely developed, the frontals are small or are largely covered by the nasals, the superior nares occupy a nearly median position, and a heavy sclerotic ring is present. On the other hand in the relatively greater size of the maxillaries, smaller orbits, and broader temporal bar, the skull is more primitive than any described form from a later period.

The skull as a whole is relatively short compared with the length of the trunk. As nearly as can be estimated its length equals little more than one-third that of the dorsal region. The skull of *Mixosaurus* seems to be relatively much longer, equalling about two-thirds the length of the trunk, while in *Ichthyosaurus* its relative length may be as great as 80 per cent.

Facial Region.—The antorbital portion of the skull (fig. 3) is elongated and narrow as in the typical Ichthyosauria. It is, however, shorter relative to the total length of the skull than in any other ichthyosaurian known to the writer, excepting the short-faced *Ichthyosaurus breviceps* from the Lower Lias of England. In *Cymbospondylus* (no. 9950) it equals about 60 per cent. of the total length of the skull, and in *I. breviceps* 55 per cent. At the same time the extent of the maxillary anterior to the orbit is relatively larger than in any other ichthyosaurian. It amounts to 48 per cent. of the length of the antorbital region in specimen 9950, while in *I. breviceps* with a somewhat shorter rostrum, in which one would expect to find the maxillary relatively long, it is less than 40 per cent. In *Mixosaurus* the length relative to the cranial region is a little less than in *Cymbospondylus.*



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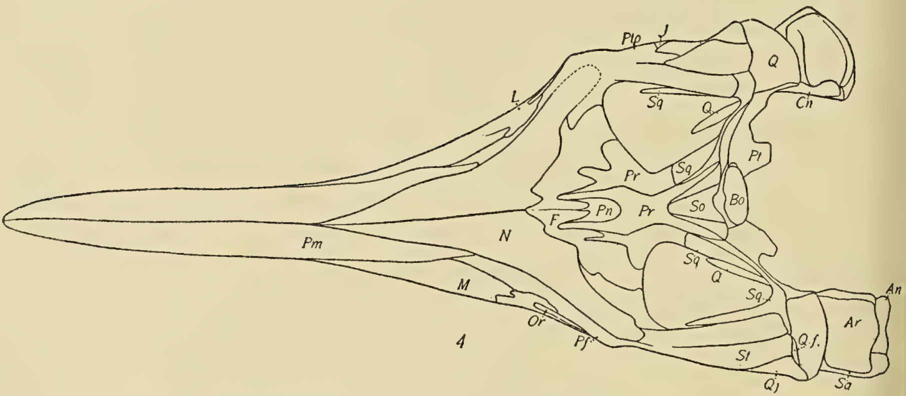

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Figs. 3 and 4. *Cymbospondylus petrinus* Leidy. Skull $\times \frac{1}{10}$. Fig. 3, side view; fig. 4, superior view. *Pm*, premaxillary; *M*, maxillary; *N*, nasal; *L*, lachrymal; *J*, jugal; *Or*, orbit; *F*, frontal; *Pf*, pre- and post-frontal; *Pto*, postorbital; *Pr*, parietal; *Pn*, pineal foramen; *Sq*, squamosal; *St*, supratemporal; *Q*, quadrate; *Qj*, quadratojugal; *Q.f.*, quadrate foramen; *Pt*, pterygoid; *So*, supraoccipital; *Bo*, basioccipital; *Ar*, articular; *An*, angular; *Sa*, surangular; *Cn*, coronoid; *Sp*, splenial; *D*, dentary.

The *premaxillaries* are greatly elongated, extending more than half the total length of the skull. For a little more than half of their length measured back from the anterior end of the rostrum they are united dorsally. Behind the region of contact with each other they are separated by the nasals.

The *maxillaries* are longer than in any other described ichthyosaurian, both in relation to the length of the rostral region and to that of the cranium; and almost, if not quite, half of the dentigerous margin of the upper jaw is situated on these elements. In *Mixosaurus* the length of the maxillaries is also relatively great.

The *superior nares* are situated much as in *Ichthyosaurus*, though apparently occupying a slightly more advanced position than in most forms.

The *nasals* (fig. 4) are large and extend back over the frontals as in other Ichthyosauria. They are relatively very widely expanded, much as in *Ichthyosaurus* and *Baptanodon*. No comparison with *Mixosaurus* has been made, as the writer has not been able to make certain of the form of this element in that genus. From Repossi's figures of the skull (Repossi, 1902, tav. 9, fig. 1) one suspects that the nasals are very large.

Fronto-Parietal Region.—As in *Ichthyosaurus* the anterior portion of the cranial region is covered by the expanded nasals. A little more of the frontal element seems to be exposed than often occurs in *Ichthyosaurus*. The large pineal foramen is surrounded mainly by the parietals, instead of wholly or to a large extent by the frontals as in *Ichthyosaurus*.

Orbital Region.—One of the most striking features of the skull in *Cymbospondylus* is the relatively small size of the orbit, compared with the orbital region of most species of *Ichthyosaurus*, or more particularly with *Ophthalmosaurus* (fig. 5). Even in specimens crushed laterally so that the height of the orbit would tend to be increased, the relative size is practically the same as in the figure above (fig. 3). (See also pl. 6.) In *Baptanodon* as figured by Gilmore[8] the length of the orbit is only a little less than one-fourth that of the whole skull, including the much elongated snout. In *Cymbospondylus* it is about one-sixth the length, in spite of the fact that the rostral region is relatively short. The relative size of the orbit is particularly noticeable in comparison with the anteroposterior diameter of the temporal bar immediately behind it. The anteroposterior diameter of the temporal bar equals over 80 per cent. of the anteroposterior diameter of the orbit in *Cymbospondylus* (no. 9950); in *Baptanodon* it appears to be less than 25 per cent. Of the undistorted *Ichthyosaurus* skulls of which the writer is able to obtain any information, the forms which most nearly approach *Cymbospondylus* in these characters are *I. platyodon* and *I. lonchiodon* of the English Lower Lias.

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[8] Gilmore, C. W., Mem. Carneg. Mus., vol. 2, pl. 7.

In *Mixosaurus* and *Shastasaurus* the orbits are relatively large, though perhaps somewhat smaller than in *Ichthyosaurus.*

The sclerotic ring of *Cymbospondylus* (pl. 5, fig. 2) has much the same structure as in *Ichthyosaurus* and *Baptanodon.* The number of plates is about sixteen to eighteen. In *Ichthyosaurus* the number ranges from fifteen to twenty. Gilmore finds but fourteen plates in *Baptanodon*, and the same number is given for *Ophthalmosaurus* by Andrews. The inner or median ends of the plates bend quite sharply over the equatorial region of the eyeball and extend for some distance over the inner side of the eye. The lateral flattening of the eyeball shown by the sharp curvature of the plates on the equator of the eye has been noted also for *Ichthyosaurus* by Owen[9] and recently on *Baptanodon* by Gilmore.[10] The relative size of the sclerotic ring agrees with that of the orbit in being smaller than in any of the later ichthyosaurs. The ring in *Ichthyosaurus platyodon* and in the short-headed *I. breviceps* is nearly half again as large as in *Cymbospondylus.*

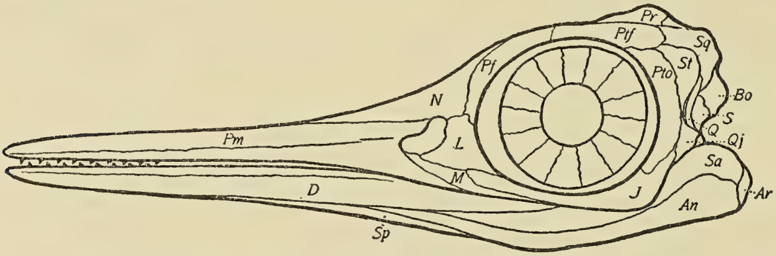

FIG. 5. *Ophthalmosaurus icenicus* Seeley. Skull. (Adapted from C. W. Andrews.) About $\frac{1}{9}$ natural size. *Pm*, premaxillary; *M*, maxillary; *N*, nasal; *L*, lachrymal; *J*, jugal; *Pf*, prefrontal; *Ptf*, postfrontal; *Pto*, postorbital; *Pr*, parietal; *Sq*, squamosal; *St*, supratemporal; *Qj*, quadratojugal; *Q*, quadrate; *S*, stapes; *Bo*, basioccipital; *Ar*, articular; *Sa*, surangular; *An*, angular; *Sp*, splenial; *D*, dentary.

Temporal Region.—The lateral temporal bar of *Cymbospondylus* is characterized by uncommon length anteroposteriorly. Its height is somewhat less than in most ichthyosaurs. Relative to the length of the cranial region it is much less elevated than in *Baptanodon*. Behind the jugal the inferior side of the temporal bar is sharply cut out so as to form with the slightly concave coronoid region of the mandible an elliptical opening with its long diameter extended anteroposteriorly. According to the suggestion of McGregor[11] the temporal bar originally contained a lateral temporal opening, which was closed through gradual anteroposterior compression of the bar owing to the enlargement of the orbit. In *Cymbospondylus* the bar shows fully as much area on the side of the skull as in many reptilian forms possessing a lateral temporal fenestra. As the quadratojugal passes above the inferior notch in the bar, it is improbable that this opening corresponds to a lateral temporal fenestra which was being lost in *Cymbospondylus* through breaking down of an inferior temporal arcade. Though there is no doubt that the temporal bar has been progressively reduced, it seems very doubtful whether it ever enclosed a lower or lateral temporal fenestra.

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[9] Owen, R., Fossil Rept. Lias Form., pt. 3 (Monog. Pal. Soc., Lond., 1881), p. 103.
[10] Gilmore, C. W., Mem. Carneg. Mus., vol. 2, p. 328.

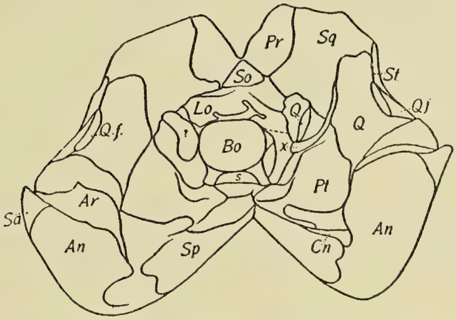

FIG. 6. *Cymbospondylus petrinus* Leidy. Skull, posterior view, × $\frac{1}{9}$. *Pr*, parietal; *Sq*, squamosal; *St*, supratemporal; *Qj*, quadratojugal; *Q*, quadrate; *Q.f.*, quadrate foramen; *So*, supraoccipital; L*o*, lateral occipital; *Bo*, basioccipital; *S*, basisphenoid; *X*, stapes?; *Pt*, pterygoid; *Ar*, articular; *Sa*, surangular; *An*, angular; *Cn*, coronoid; *Sp*, splenial.

Occipital Region.—The occipital region of *Cymbospondylus* (fig. 6) seems to be well enclosed with bone and the posterior temporal openings are small. The basioccipital differs from that of other ichthyosaurians in presenting a strongly concave articular face for contact with the convex anterior face of the atlas. The inferior side of the basioccipital is characterized by the development of prominent hypapophyses similar to those of *Sphenodon*. The form of the lateral occipitals is not well known, but they seem to be perforated by large lateral foramina. The supraoccipital extends forward a considerable distance to form a part of the floor of a deep fossa between the posterior arms of the parietals. The form of the opisthotic and prootic are not certainly known. The stapes is not certainly recognized. If represented by an element which lies between the otic region and the quadrate (fig. 6, *x*) it is much smaller and more slender than in the later ichthyosaurs. It may also be noted that no distinct pit for the reception of the distal end of the stapes is visible on the inner side of the quadrate.

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[11] McGregor, J. H., Mem. Amer. Mus. Nat. Hist., vol. 9, p. 91.

Quadrate and Suspensorium.—The quadrate is large and heavy and seems to be closely and broadly united with the adjoining elements, making the posterior angles of the skull particularly firm. The anterior side of the quadrate overlapping the pterygoid extends forward as a broad plate resembling that seen in the Rhynchocephalia. The face articulating with the mandible is crossed obliquely by a marked depression situated between two strongly convex faces. This form of the articular face on the quadrate has recently been noted also in *Ichthyosaurus platydactylus* by Broili,[12] and is suggested in *Sphenodon*.

The large quadrate foramina perforating the posterior angles of the skull are situated much as in the later ichthyosaurs. The quadratojugal forming the outer boundary of the quadrate foramen is overlapped superiorly by the supratemporal. The inferior border of the quadratojugal extends forward and above the inferior temporal notch to meet the jugal.

Palatine Region.—The palate of *Cymbospondylus* (fig. 7) closely resembles that of *Ichthyosaurus* in most details of its structure. The roof of the mouth is largely covered by the expanded palatines and pterygoids, the median margins of the pterygoids approaching each other closely for a considerable distance back toward the basisphenoid. The pterygoids are characterized by prominent posterior projections of the median edges, which extend some distance back of the basioccipital. In specimen 9950 the posterior portion of the lateral wing on each of the pterygoids is separated from the main body of the bone in such a manner as to suggest that it represents a distinct element (fig. 7, *x*). If there is a separate bone here it is evidently a discrete ectopterygoid which has united with the pterygoid in all later forms.

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[12] Broili, F., Paleontg., Bd. 54, p. 140.

Mandible.—The lower jaw of *Cymbospondylus* is formed much as in the later ichthyosaurian genera, the relations of the several elements as they appear on the outer side of the rami being much as in *Ichthyosaurus*. In the genus *Merriamia* (fig. 8) possibly also in *Mixosaurus*, the surangular is relatively large and forms the principal part of the outer side of the posterior half of the jaw. In *Cymbospondylus* it forms the anterior side of the cotylus for the

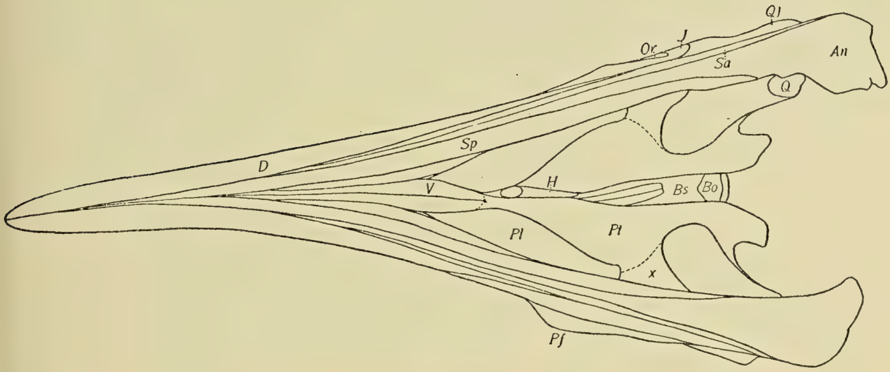


FIG. 7. *Cymbospondylus petrinus* Leidy. Skull, inferior view, $\times \frac{1}{10}$. *D*, dentary; *Sp*, splenial; *Sa*, surangular; *An*, angular; *Or*, orbit; *J*, jugal; *Qj*, quadratojugal; *Q*, quadrate; *Bo*, basioccipital; *Bs*, basisphenoid; *Pt*, pterygoid; *X*, ectopterygoid?; *H*, hyoid; *Pl*, palatine; *V*, prevomer?

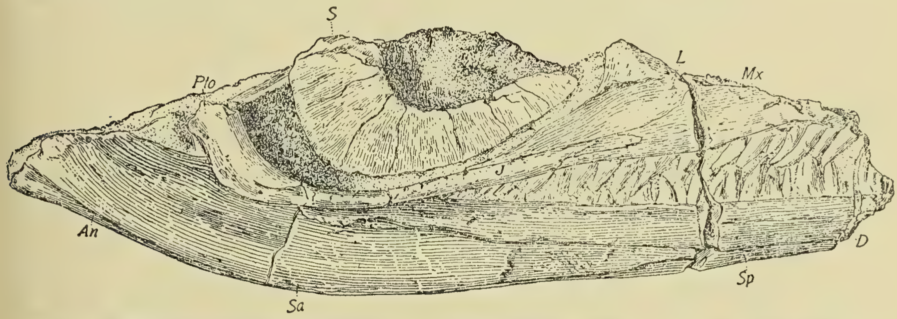


FIG. 8. *Merriamia zitteli* (Merriam). Skull, lateral view, $\times \frac{3}{5}$. *An*, angular; *Sa*, surangular; *Sp*, splenial; *D*, dentary; *Mx*, maxillary; *L*, lachrymal; *J*, jugal; *Pto*, postorbital; *S*, sclerotic ring.

quadrate, and is thickened transversely anterior to the cup. As in the other ichthyosaurian genera there is no coronoid elevation, but the surangular presents a broad flat superior surface in the region of the coronoid. Below the coronoid margin there is, as in *Baptanodon*, a relatively small lamellar bone extending back almost to the posterior extremity of the inner side of the jaw (fig. 9), and representing the coronoid or the prearticular. The articular extends from the cotylus to the posterior end of the mandible. It is much thickened immediately behind the cotylus, and is thickened also at the posterior end. Between these regions the upper surface is strongly hollowed.

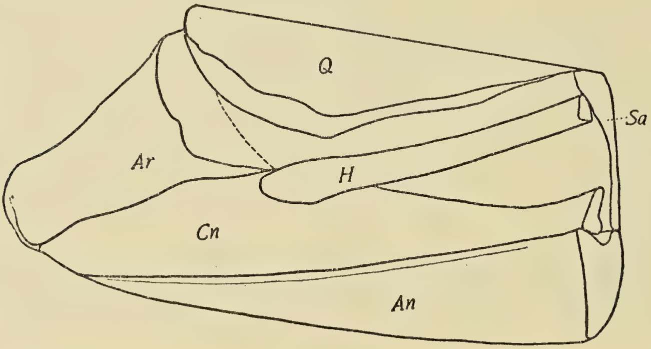
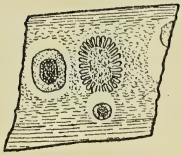


FIG. 9. *Cymbospondylus petrinus* Leidy. Inner side, posterior end of left ramus of mandible, × ⅓. *Ar*, articular; *Cn*, coronoid; *An*, angular; *Sa*, surangular; *H*, hyoid; *Q*, quadrate.

Dentition

In the specimens of *Cymbospondylus* that have been examined thus far the dentition has not been materially different from that of *Ichthyosaurus* excepting in the insertion of the teeth (figs. 10 to 12). The numerous teeth are all simple conical, and are, in some cases at least, set in distinct pits. The base of the dentine cone is strongly folded (fig. 10), and there does not appear to be any considerable amount of cement covering it. As nearly as can be determined there were thirty to thirty-five, or more, teeth in each ramus of the jaws. Between the anterior and posterior ends of the jaws there is a slight difference in form, the posterior teeth being somewhat shorter and heavier (fig. 3). This is also true of the genus *Merriamia* (fig. 8), of which the dentition of the posterior half of the jaws is known. In *Merriamia* and in *Shastasaurus* the teeth, as far as known, are set in open grooves. Imperfect alveoli may, however, have been present in some of the regions of the jaw which have not yet been examined.

The characters seen in the American Triassic forms are in strong contrast to the nature of the dentition of *Mixosaurus* (figs. 13 and 14), in which the teeth show marked differentiation and are set in rather widely spaced distinct pits.



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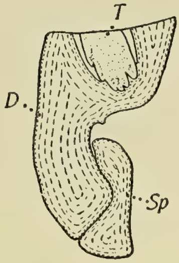

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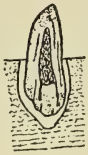

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Fig. 10. *Cymbospondylus petrinus* Leidy. Horizontal cross-section of dentary about 5 mm. below upper margin, showing teeth set in completely surrounded bone sockets, × ½.

Figs. 11 and 12. *Cymbospondylus petrinus* Leidy. Fig. 11, transverse cross-section of lower jaw showing teeth set in sockets in the dentary. Superior margin cut down several millimeters. *T*, tooth; *D*, dentary; *Sp*, splenial, × ½. Fig. 12, anteroposterior cross-section of the base of a tooth set in the dentary, × ½.

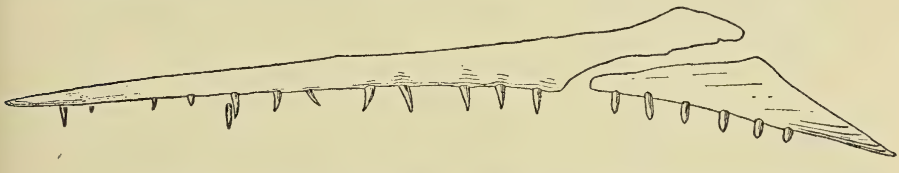


Fig. 13. *Mixosaurus cornalianus* (Bassani). Upper jaw and dentition, × ¾. (Adapted from Repossi.)

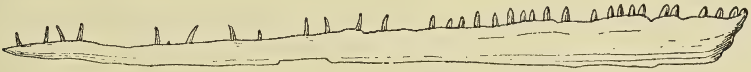
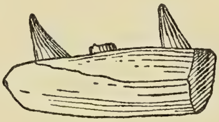


Fig. 14. *Mixosaurus cornalianus* (Bassani). Lower jaw and dentition, × ¾. (Adapted from Repossi.)

As has been shown by Fraas (1891, p. 38) the dentition of *Mixosaurus* (?) *atavus* (figs. 15 and 16) is characterized by extreme differentiation of the teeth, by their firm insertion in slightly separated alveoli, by the coarse folds of the basal portion of the dentine cone, and by the extreme reduction of the cement.

The peculiar characters of the dentition of *Mixosaurus*, occurring as they have with other features which undoubtedly indicate a primitive stage of evolution, have suggested that possibly the dentition is essentially primitive, and that an original differentiated stage of a thecodont dentition which developed in the ancestors of the ichthyosaurs has been lost in the adaptation of the later forms, but is retained in the primitive *Mixosaurus*. If, as appears to be the case, the dentition of *Cymbospondylus* is not differentiated more than that of *Ichthyosaurus*, it may be that the differentiation of the mixosaur dentition was acquired in adaptation to a peculiar food habit; while the thecodont insertion, here as in most of the Triassic forms, may be a persistent or primitive character.



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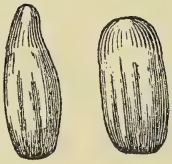

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Fig. 15. *Mixosaurus* (?) *atavus* (Quenstedt). Anterior end of lower jaw with dentition, natural size. (After Quenstedt.)

Fig. 16. *Mixosaurus* (?) *atavus* (Quenstedt). Two forms of teeth from the lower jaw, natural size. (After Fraas.)

Vertebrae

Vertebral Formula.—In the typical Ichthyosauria of the Jurassic the number of vertebrae in the spinal column shows considerable variation. In the genus *Ichthyosaurus* variation occurs principally in the posterior caudal region through the addition of small centra in the pinnigerous portion of the tail. The presacrals in *Ichthyosaurus* pretty constantly number between 40 and 46 with some slight variation from this number. An exception is found in the peculiarly specialized *I. platydactylus* Broili of the Cretaceous, in which the pelvis appears to have been near the 54th centrum. In *Baptanodon reedi* Gilmore the region of the pelvis is indicated at the 49th or 50th centrum, as the transverse processes reach their lowest position on the sides of the centra at this point. In *Ophthalmosaurus* there are 40 presacrals, according to Andrews.[13]

Of the Triassic genera the complete presacral segment of the column is known only in *Mixosaurus* and *Cymbospondylus*. Judging from Repossi's figures there are between forty-five and fifty presacrals present in *Mixosaurus*. In a specimen of *Cymbospondylus* (pl. 7, fig. 1; no. 9950), including the complete presacral region, there are not less than 65 presacrals. In the type of *Delphinosaurus* (pl. 7, fig. 2) there are 40 presacrals present, and enough of the cervical region is absent to increase the number to between 45 and 50. In specimen 10998 (pl. 7, fig. 3) the vertebral column is complete to the posterior part of the skull, and there are about 40 presacrals present. As the region of the back of the skull is imperfectly preserved, there are probably several vertebrae not recognized, so that the total may be supposed to be the same as in the type specimen. In *Shastasaurus osmonti* (fig. 57) there are at least thirty-six vertebrae anterior to the region in which the rib articulation moves down from the upper portion of the lateral face of the centrum. As this downward movement occurs in all other ichthyosaurians near the middle of the dorsal region and generally fifteen or more vertebrae anterior to the pelvis (*Delphinosaurus* 15, *Cymbospondylus* 19 or more, *Ichthyosaurus* 15 or more) at least fifteen centra may be added to the thirty-six known in *Shastasaurus* making the number near 50. It appears then that in the known Triassic forms the number of presacrals is generally somewhat larger than in the typical *Ichthyosaurus*. That the number should be larger in these forms than in most of the later ichthyosaurs is rather remarkable, since the primitive reptilian types as the Diaptosauria and the Phytosauria, which have been suggested as ancestral to the Ichthyosauria, have in nearly all cases less than thirty presacrals.

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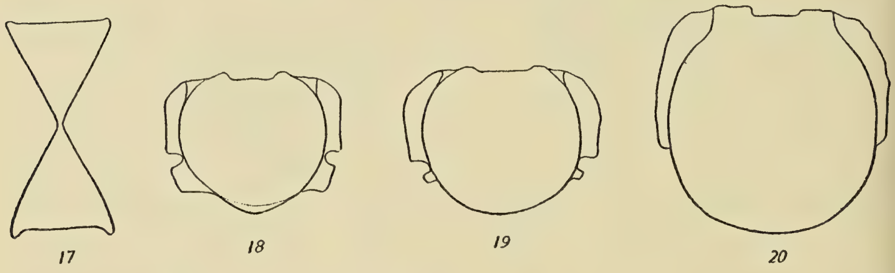
[13] Andrews, C. W., Geol. Mag., Dec. 5, vol. 4, p. 205.

The total number of vertebrae in the caudal region including the smaller centra at the end of the pinnigerous portion seems to be very closely represented in a *Delphinosaurus* specimen (no. 10998), and is approximately 75. In one of the Milan specimens of *Mixosaurus* the writer has counted about seventy-six vertebrae behind the posterior limb. In a large specimen of *Cymbospondylus* (fig. 132, no. 9947) a continuous series of 54 vertebrae is present behind the pelvis, and a part of the distal region of the tail is absent.

In the caudal region the number of vertebrae anterior to the characteristic bend in the tail is, so far as known, nearly the same as in the later forms, or in some cases somewhat smaller. In the Milan

Mixosaurus specimen possessing seventy-six caudals, the bend occurs near the twenty-fifth centrum behind the pelvis. On one specimen of *Delphinosaurus* (pl. 7, fig. 2) it is situated between the 25th and 30th vertebrae behind the pelvis, and in another (pl. 7, fig. 3) it appears to be between the 25th and 35th centra. In *Cymbospondylus* (fig. 132) the bend in the caudal region occurs at the 30th to 35th centrum behind the pelvis as it is situated here. This number is nearly the same as the number of centra that ordinarily intervenes between the pelvis and the downward bend of the tail in *Ichthyosaurus*.

Form of Centra.—The individual vertebral centra of all Triassic ichthyosaurians are biconcave as in later types. The biconcavity is so deep in some forms, as in the posterior dorsals of *Cymbospondylus* (fig. 24) or in the caudals of some of the small species from the Upper Triassic of Shasta County, that the middle portion of the centrum is perforated by a very small canal. The same character has been noted in the vertebrae of *Mixosaurus* (?) *atavus* by Fraas (1891, pp. 38 and 39) and was described by von Meyer[14] for a Triassic vertebra probably belonging to an ichthyosaurian. Somewhat similar perforations appear occasionally in some of the later ichthyosaurs as in *Ichthyosaurus campylodon.*[15] In most forms the character of the excavation is similar to that in the typical species of *Ichthyosaurus* (fig. 17), the concavity beginning near the periph-



FIGS. 17–20. *Shastasaurus osmonti* Merriam. Outlines of cervical and dorsal vertebrae, × $\frac{2}{5}$. Fig. 17, anteroposterior section of 36th centrum; fig. 18, anteroposterior profile of 4th centrum; fig. 19, anteroposterior profile of 12th centrum; fig. 20, anteroposterior profile of 36th centrum.

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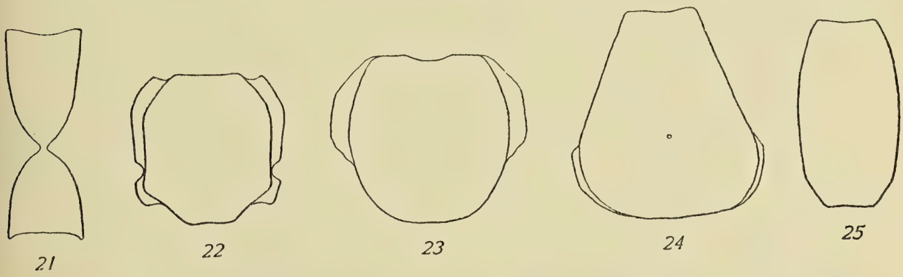
[14] von Meyer, H., Palaeontographica, Bd. 1, p. 253.

[15] Kiprijanoff, W., Mém. l'Acad. Imp. des Sc., St. Petersb., 7 ser., t. 28, no. 8, p. 77. See also Dames, W., Zeit. d. deutsch. geol. Gesel., 1893 Bd. 45, p. 30.

ery of the centrum and sloping evenly toward the center. In *Cymbospondylus petrinus* (fig. 21), the best known Middle Triassic form, the outer portion of the articular face is nearly flat or only slightly hollowed, and the excavation cuts in sharply at about half of the distance to the middle. The flattening of the peripheral portion of the terminal faces is very pronounced in the posterior dorsal region.

The occurrence of vertebrae in which the terminal faces are largely filled out in some of the earliest known ichthyosaurs naturally raises a question as to whether the deeply biconcave centra of the Upper Triassic and later genera are primitive, or whether they have been secondarily developed as a part of the adaptation to aquatic life. The more nearly solid centrum is evidently in general the type best fitted to meet the requirements in active land or shore forms. It has appeared in many of the reptilian groups, and even in certain of the more highly specialized Stegocephalia. Its development is possibly to some extent a function of size in the individual among land forms, as is indicated by its appearance in the large Stegocephalia and many reptiles; the deeply biconcave vertebrae persisting principally in the small land reptiles. In aquatic forms in which the vertebral column is relieved of a part of the strain of supporting the body the biconcave type of centrum may prove adequate. Of the specimens of the earliest European ichthyosaurs examined by the writer none have, however, been found to show such a degree of marginal flattening as is seen in *Cymbospondylus*, excepting the doubtful vertebrae described by von Meyer (Palaeontg. B. 1, p.



Figs. 21–25. *Cymbospondylus petrinus* Leidy. Outlines of vertebrae, $\times \frac{1}{4}$. Fig. 21, anteroposterior cross-section of a dorsal centrum; fig. 22, anteroposterior profile of 3rd centrum; fig. 23, anteroposterior profile of anterior dorsal centrum; fig. 24, anteroposterior profile of posterior dorsal centrum; fig. 25, anteroposterior profile of posterior caudal centrum

253). In the earliest forms from the Middle Triassic the centra are generally deeply biconcave, the concavity beginning at or close to the margin of the centrum. In *Mixosaurus* (fig. 121) a slight marginal flattening may be present, but it is not comparable to that of *Cymbospondylus*. As yet the extreme flattening in *Cymbospondylus* has been observed only on specimens of the large *C. petrinus*. In the type of *C. piscosus* (fig. 136) the concavity of the centra is like that commonly seen in *Ichthyosaurus*, so that large size may be an important factor in this case. On the other hand the enormous centra of *Shastasaurus careyi* from the Upper Trias exhibit no filling out of the intervertebral space. Among the more recent ichthyosaurians both perforation of the centrum and flattening of the peripheral portion of the terminal faces are occasionally seen, and appear together in *Ichthyosaurus campylodon*.

The proportions of the vertebral centra in the different regions of the column are in general much as in the ichthyosaurs of the Jurassic. The centra are generally broader than high in the cervical region, and gradually increase in height to the middle dorsal region, where the vertical and transverse diameters are nearly equal (figs. 18–20). Behind this point the transverse diameter becomes relatively small until in the posterior caudal region of some forms the height may equal three or four times the width.

In the cervical and anterior dorsal regions the rib articulation extends upward over the superior margin of the centrum and covers a part of the base of the upper arch (fig. 26). In the posterior dorsal region it moves down to the lower margin, but rises again to about half the height of the side of the centrum near the middle caudal region. Particularly in *Cymbospondylus petrinus* (fig. 24) the posterior dorsal centra take on a sharply triangular form where the rib articulations reach the lower margin of the centrum.

The relative length of the anteroposterior diameter varies greatly among the Triassic genera. In some, particularly the latest, largest and most generally specialized forms the centra are relatively short and high, as is exemplified in *Shastasaurus careyi* (fig. 29), in which the length of a middle dorsal may equal less than 29 per cent. of the height. In all of the earlier forms the centra are relatively long. In *Delphinosaurus perrini* (fig. 27), found principally in a lower horizon than the forms with very short centra, the length of middle dorsal centra may equal 84 per cent. of the height. The relatively great increase in height and width of the dorsal centra is paralleled to a considerable extent in the Cetacea. The extraordinary height of the centrum has been considered by McGregor[16] as the probable reason why the ribs of ichthyosaurs do not articulate on the upper arches. It is true that in the small forms with relatively long and low centra, as in *Delphinosaurus*, the rib heads rest against the upper arches to a considerable extent. It is also true that in several species of *Shastasaurus*, with vertebral centra as

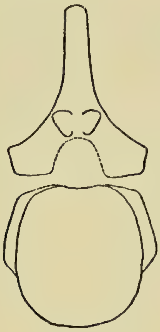


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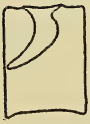
FIG. 26. *Delphinosaurus perrini* Merriam. Anteroposterior profile of anterior dorsal vertebra, × ½.



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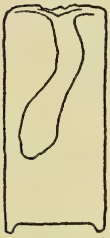

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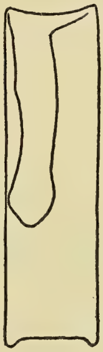

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FIG. 27. *Delphinosaurus perrini* Merriam. Lateral view of middle dorsal centrum, × ⅓.
FIG. 28. *Shastasaurus osmonti* Merriam. Lateral view of middle dorsal centrum, × ⅜.
FIG. 29. *Shastasaurus careyi* (?) Merriam. Lateral view of middle dorsal centrum, × ⅜.

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[16] McGregor, J. H., Mem. Am. Nat. Hist., vol. 9, pt. 2, p. 91.

high and thin as in the typical *Ichthyosaurus*, the rib heads of the cervical and anterior dorsal region are in contact with the base of the neural arch.

Neural Arches.—The upper arches of the vertebrae in the Triassic genera seem in every case to be thicker transversely than in the typical *Ichthyosaurus*. The neural spines of the vertebrae of *Mixosaurus* (fig. 123), as figured by Repossi, appear to be thin and flattened distally, but a prominent rib is present along the lateral face of the arch, and extends for a considerable distance up on the side of the spine. In the cervical region of all the American Triassic forms the neural spines are so thick as to be nearly round in cross-section. In the dorsal region the spines may be greatly broadened anteroposteriorly and become quite thin distally (fig. 32*b*). This change from thick spines on the cervicals to broad, thin ones on the dorsals is well shown in *Delphinosaurus perrini* (pl. 7, fig. 2), but even in this form the lateral faces of the spines on the dorsals are each marked by a well-developed ridge (fig. 30). This lateral rib is situated in the middle of the lateral face of the spine, and possibly represents the original column of the spine from which the anteroposterior expansion has developed.

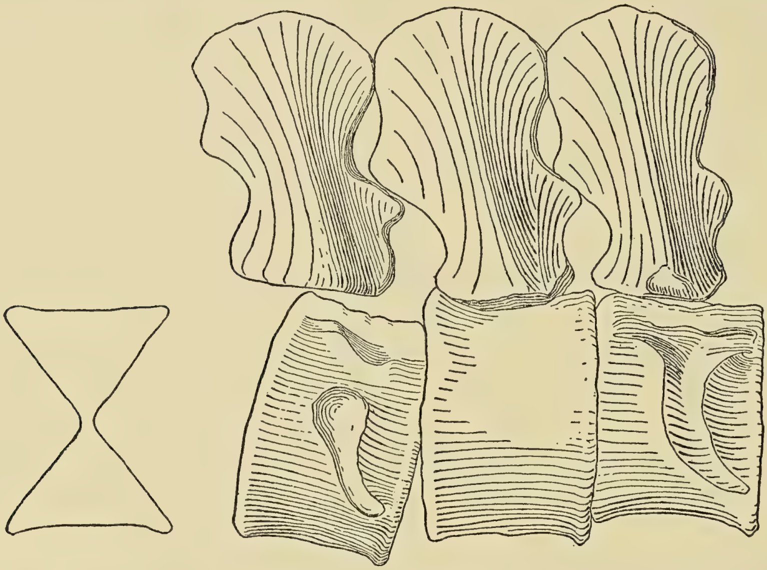
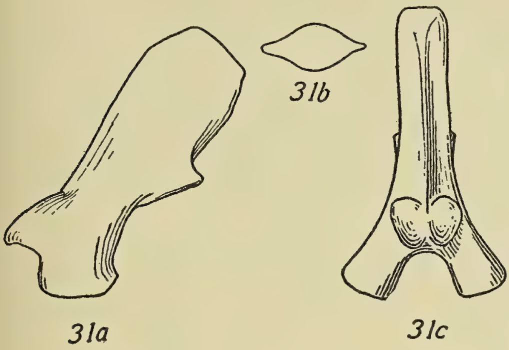
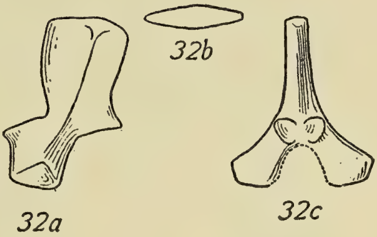
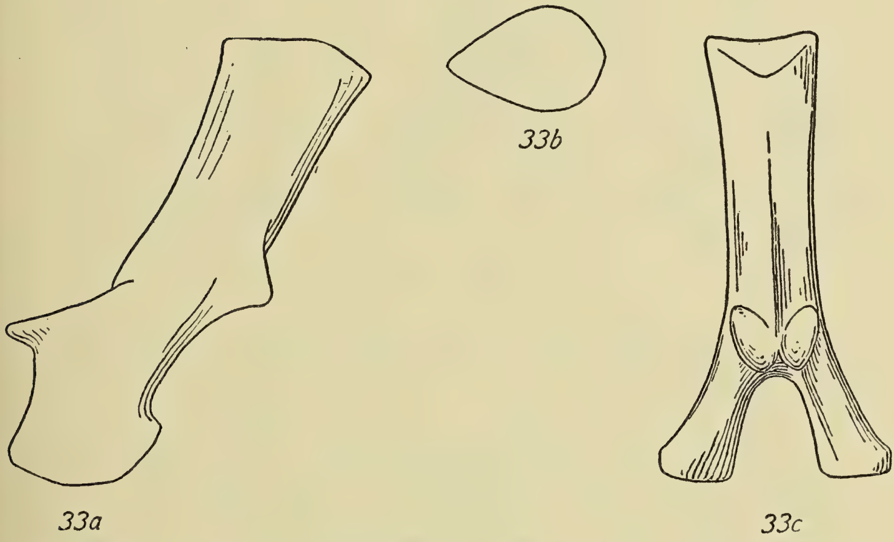


Fig. 30. *Delphinosaurus perrini* Merriam. Middle dorsal vertebrae situated at the point in the series where the diapophysial and neurapophysial surfaces of articulation are separated, × ¾.

In *Shastasaurus altispinus* and *S. careyi* the spines show little transverse flattening in the dorsal region and sometimes none at all; but may be considerably thickened and perfectly circular in cross-section distally. In the type specimen of *S. altispinus* the





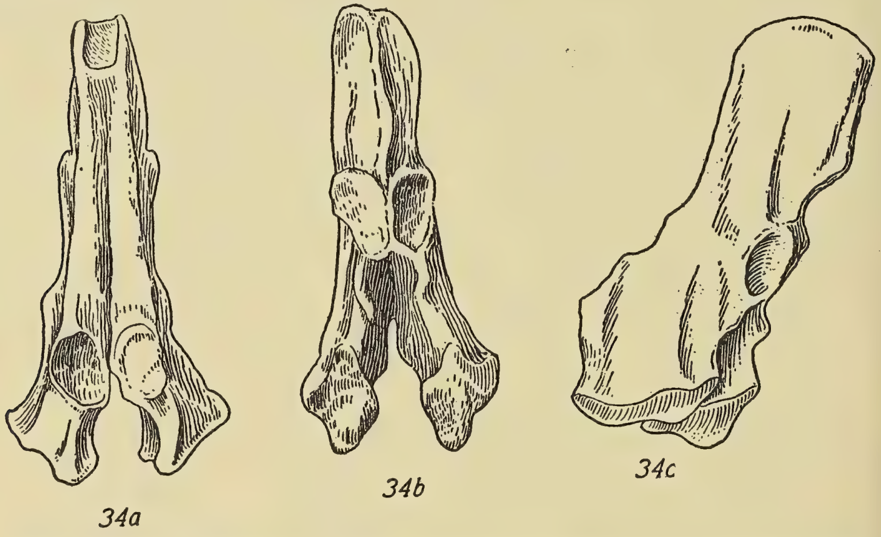


FIGS. 31*a*–31*c*. *Shastasaurus osmonti* Merriam. Neural arch of a dorsal vertebra, × ½. Fig. 31*a*, lateral view; 31*b*, cross-section of summit of neural spine; 31*c*, anterior view.

FIGS. 32*a*–32*c*. *Delphinosaurus perrini* Merriam. Neural arch of a dorsal vertebra, × ½. Fig. 32*a*, lateral view; 32*b*, cross-section of summit of neural spine; 32*c*, anterior view.

FIGS. 33*a*–33*c*. *Shastasaurus altispinus* Merriam. Neural arch of a dorsal vertebra, × ½. Fig. 33*a*, lateral view; 33*b*, cross-section of summit of neural spine; 33*c*, anterior view.

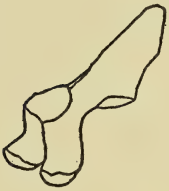
middle dorsal spines seem to have thin, blade-like anterior and posterior expansions of no great width, for a short distance above the zygapophyses (pl. 18, figs. 2*a* and 2*b*). In a specimen of *S. careyi* (pl. 18, figs. 5*a* to 5*c*) the distal end of the spine is considerably thicker than the middle section, and shows no anterior or posterior blade-like expansions, but is circular in cross-section. In *S. altispinus* the terminal portion of the spine is hollowed out by an anteroposterior groove. In *S. careyi* it is evenly convex or domed.



Figs. 34*a*–34*c*. *Mixosaurus* (*?*) *atavus* (Quenstedt). Neural arch of an anterior dorsal vertebra, natural size. (After Fraas.) Fig. 34*a*, anterior view; 34*b*, posterior view; 34*c*, lateral view.

In view of the fact that thickening of the neural spines is the rule among the Triassic Ichthyosauria, and is most persistent in the anterior portion of the vertebral column where the development of a sculling tail would have the least influence on the character of the neural spines, it is probable that the arches of the ancestral forms were of the round or thickened rather than of a laterally compressed type. The rounded type is occasionally found in aquatic forms, but is most common among running types.

In the cervical, dorsal, and anterior caudal regions zygapophysial facets are developed on the upper arches of all Triassic ichthyosaurs. As was first noted by Fraas (1891, p. 39), the facets of the zygapophyses in *Mixosaurus* (?) *atavus* differ from those of *Ichthyosaurus* in being distinctly separated and not situated in the same plane (figs. 34*a* to 34*c*). In the Jurassic forms the two faces are brought together at the median line and unite to form a single face (fig. 35). In all of American Triassic forms (figs. 31–33 and 36) the zygapophysial facets are large, distinctly separated, and inclined away from each other in the cervical and anterior dorsal region. In the posterior dorsal and caudal regions the facets may be considerably reduced and fall into nearly the same plane. This difference is evidently due to the fact that in the development of a broad, vertical sculling organ, the principal movements of the body have been sideways, and a union of the zygapophysial facets in one plane facilitated this movement. The normal form of zygapophysial articulation in which the anterior facets look toward each other would interfere to some extent with this motion. In the evolution of the group the tendency to change the zygapophyses naturally appeared first in the caudal region and was gradually carried forward toward the neck region. In the Middle Triassic forms the sculling tail was well developed and the zygapophyses of the posterior region of the column had already been considerably modified. In the cervical, and to some extent in the anterior dorsal region, the modification had not been very strongly expressed. The evidence of the zygapophyses can scarcely be interpreted as pointing toward any other than a land or shore type as the ancestral form of the group.



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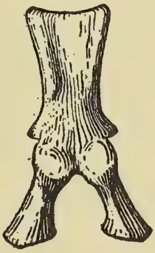

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FIG. 35. *Ichthyosaurus quadriscissus* Quenstedt. Neural arch with united zygapophyses × ½. (After Fraas.)

FIG. 36. *Cymbospondylus petrinus* Leidy. Neural arch of 5th cervical vertebra, anterior view, × ½.

Hypocentral Elements.—The inferior or hypocentral elements of the caudal region furnish a most characteristic feature of all Triassic genera, and represent a less advanced stage in the development of the ichthyosaurian tail fin than in the post-Triassic forms. In every case where they have been observed the caudal hypocentra are united ventrally to form a long median stem (fig. 37), giving the inferior arches the Y-shaped form seen in the lower arches of the caudal series in most reptiles. In the type specimen of *Delphinosaurus perrini* (pl. 7, fig. 2) the chevrons are present from the anterior caudal region at least as far back as the bend in the tail.

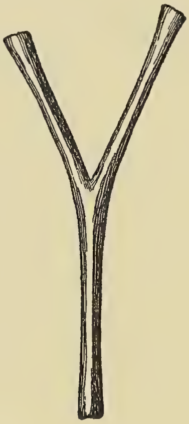

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Fig. 37. *Delphinosaurus perrini* Merriam. Inferior arch of anterior caudal vertebra, × $\frac{3}{4}$.

In the ichthyosaurs of the Lower Lias of Europe (fig. 48, p. 256) the hypocentral elements are present, in many cases at least, considerably beyond the bend in the tail. According to Owen[17] they are not present on the terminal twenty or more vertebrae in *Ichthyosaurus*. In some of the Upper Liassic ichthyosaurs of South Germany, particularly in *I. quadriscissus* (fig. 49, p. 257), lower arches are not present in the region of the tail immediately in front of the bend, and have evidently in some cases disappeared entirely. In *Ophthalmosaurus*, according to Andrews,[18] caudal intercentra appear to be present. In *Baptanodon*, according to Knight,[19] the lower arches are absent.

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[17] Owen, R., Foss. Rept. Lias. Form., 1870, p. 92.

[18] Andrews, C. W., Geol. Mag., Dec. 5, vol. 5, p. 205.

[19] Knight, W. C., See Gilmore, Mem. Carnegie Mus., vol. 2, p. 107.

The history of the Ichthyosauria seems to give us a pretty definite trend of evolution of the hypocentral elements of the caudal region (figs. 43 to 49). It begins in the Triassic with forms in which the lower arches are of the normal chevron type. In the Lower Liassic ichthyosaurs the inferior union of the short paired elements has ceased. In the Upper Lias the hypocentra may disappear largely or in part, and in *Baptanodon*, one of the most recent genera of the order, they seem to have disappeared entirely.

The gradual modification and final elimination of the caudal hypocentra is undoubtedly to be ascribed to the increased efficiency of the terminal caudal fin. In the earlier ichthyosaurs the whole tail served as a sculling oar, and the elongated inferior arches heightened or broadened the tail. In later forms the flexure of the terminal portion of the caudal series made possible the development of a broad sculling organ in the region where it was most effective, and the power came to be applied largely in that region.

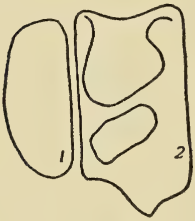
In the cervical region of *Shastasaurus* (fig. 57, p. 263) there are facets for an intercentrum between the third and fourth centra, making a fourth intercentrum not present in *Ichthyosaurus*. In this respect *Shastasaurus* may be considered more primitive than later genera. In the older *Cymbospondylus* there is, however, no intercentrum between the third and fourth vertebrae (fig. 58). The hypocentral elements of the cervical region are not known to be materially different from those of the Jurassic forms.

Atlas and Axis.—The atlas and axis are distinctly separated in all Triassic ichthyosaurs as far as known. In *Cymbospondylus* and *Shastasaurus* the adjacent faces of the atlas and axis are both concave and there is no suggestion of fusion as in the later ichthyosaurs. The atlas of *Cymbospondylus petrinus* (pl. 8 and text fig. 38) has about the same width and height, and about three-fourths the anteroposterior diameter of the axis. The anterior face is strongly convex, the inferior and lateral borders being much thinner than the superior side. The anterior face of the atlas shows no concave face into which the basioccipital might be received, but the posterior face of the basioccipital is deeply excavated for the reception of the atlas. The narrowed lateral borders have elevated anterior and posterior edges and show no indication of the presence of rib articulations. The upper arches of the atlas are formed much as in *Ichthyosaurus*.

In *Shastasaurus* (fig. 57) the form of the atlas is much as in *Cym-*

bospondylus, though the lateral borders are evidently not as sharply set off from the anterior face by an elevated anterior edge. A portion of an upper arch, apparently belonging to the atlas in the type specimen of *S. alexandrae*, resembles the neurocentral elements of *Ichthyosaurus*.

The axis of *Cymbospondylus* is in general like the succeeding cervicals, excepting in its marked inferior truncation for the hypocentral elements. It is characterized in some of the specimens examined (pl. 8, fig. 6) by the absence of parapophyses. The diapophyses of the axis are like those of the third centrum. The third vertebra shows large parapophyses. In *Shastasaurus* the rib articulation of the axis resembles that of the corresponding element in the later ichthyosaurs, and large parapophyses as well as diapophyses are present. Excepting in the two genera described above, the atlas and axis are not well known in the Triassic forms.



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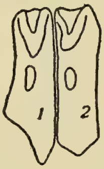

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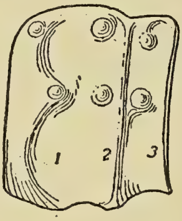

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Fig. 38. *Cymbospondylus petrinus* Leidy. Atlas and axis, lateral view, × ⅓. 1, atlas; 2, axis.

Fig. 39. *Ichthyosaurus longifrons* Owen. Atlas and axis, lateral view, × ½. 1, atlas; 2, axis. (Adapted from Owen.)

Fig. 40. *Ichthyosaurus platydactylus* Broili. Atlas, axis, and 3rd cervical, lateral view, × ⅓. 1 and 2, fused atlas and axis; 3, 3rd cervical centrum. (After Broili.)

In the genus *Ichthyosaurus* the first two elements of the vertebral column are characterized generally by partial or complete fusion with each other and, so far as the information is available, there seems to be no indication of an intervertebral space remaining. The atlas and axis are also of nearly the same size (fig. 39).

In the latest members of the ichthyosaur group, as in *Baptanodon*, the fusion of the first two elements is complete, and the hypocentral element between them may disappear or lose its identity. In *Ichthyosaurus platydactylus* as recently described by Broili[20]

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[20] Broili, F., Palaeontog., Bd. 54, p. 143.

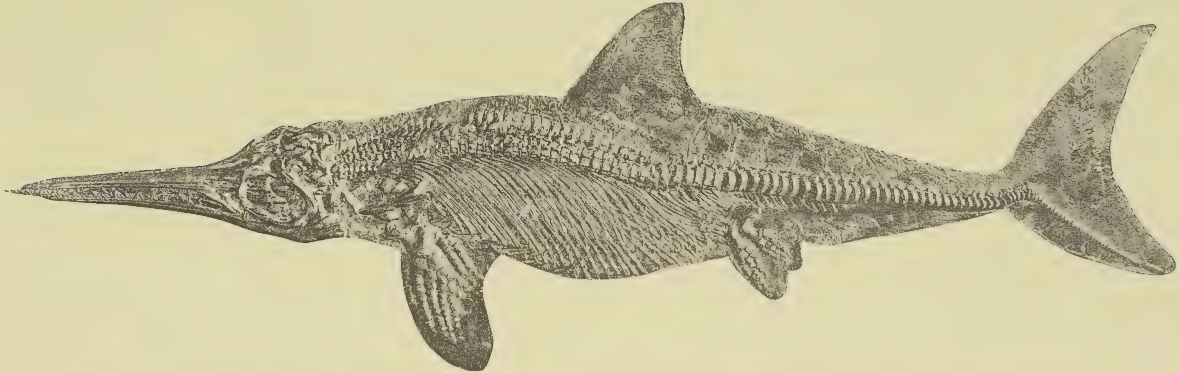

FIG. 41. *Ichthyosaurus acutirostris* Owen. Reversed photograph of a specimen in the Carnegie Museum. Reproduced by courtesy of Dr. W. J. Holland.

(fig. 40), not only have the atlas and axis fused, but the third centrum is united with the second. In all of the Jurassic ichthyosaurs the centrum of the atlas is nearly or quite as large as the centrum of the axis (fig. 39), while the neurocentra rest upon it much as the elements of the upper arch of the axis. In this respect the atlas in these forms may be said to be more specialized than in most other reptiles. A possible explanation of the peculiar form and large size of the most anterior centrum here is that the anterior cervical centrum of the later ichthyosaurs may correspond to the axis of the earlier forms, the atlas having disappeared.

The known series of forms exhibiting the structure of the anterior portion of the vertebral column of the Ichthyosauria shows pretty clearly that progressive modification of the cervical region has taken place along somewhat the same lines that have been followed in the Cetacea. In the whales, fusion of the cervicals has reached an extreme stage, and the neck may be presumed to be much shortened. In view of the considerable difference between the Triassic and the Jurassic ichthyosaurs in the form and to some extent in the function of the most anterior centrum, it is possible that in a modification of the cervical region best adapting it to aquatic life, the neck has been shortened partly by elimination or by extreme reduction of the most anterior elements.

Caudal Fin.—In no other group of the reptilia have the functions of locomotion been so largely transferred from the limbs to the tail as we find them to be in the typical ichthyosaur. In consequence of this, the caudal fin of these forms has become the most specialized sculling tail known in the Reptilia. That it has reached the stage of evolution seen in the typical *Ichthyosaurus* (fig. 41) by passing through grades of development not unlike those of some of the more generalized shore or fresh-water forms has been evident, but comparatively little information regarding the course of its evolution has been available.

In a specimen of *Ichthyosaurus trigonus posthumus* Wagner from the Upper Jurassic, one of the most recent of the well-preserved ichthyosaur specimens[21] exhibiting the impression of the epidermal investment of the caudal region, the caudal fin is seen to be broadly two-lobed with the distal end of the vertebral column turned sharply downward into the lower lobe (fig. 42). Traces of upper arches are seen on the vertebrae in the lower lobe of the fin, but lower arches seem to have been absent. The vertebral centra of the tail fin are very much smaller than those immediately in advance of the bend. They are also relatively very much longer anteroposteriorly, while the median portion is considerably constricted. The margins of the centra are thickened and rounded. Practically the same relations of the caudal vertebrae are seen in *I. platydactylus* Broili[22] of the Cretaceous. In some of the best specimens of *Ichthyosaurus* from the Upper Lias of South Germany (fig. 49), the downward bend is very pronounced, while the upper and lower vertebral arches are much reduced. The centra beyond the point of strongest curvature are not relatively much if any elongated. In these types the portion of the tail included in the terminal fin is large and the fin itself must have been capable of exerting considerable power. It was not supported to any extent by spinous projections of the upper or lower arches, but obtained

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[21] Bauer, F., Palaeontog., Bd. 44, 1897–98, p. 309, and Taf. 27.

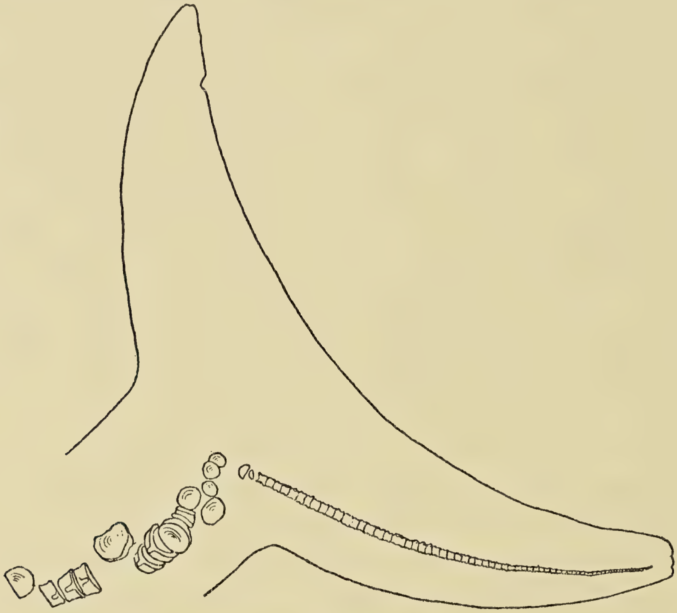

Fig. 42. *Ichthyosaurus trigonus posthumus* Wagner. Posterior caudal region with outline of the caudal fin, about $\frac{1}{10}$ natural size. (After Bauer.)

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[22] Broili, F., Palaeontog., Bd. 54, p. 147.

its width largely through the bend in the caudal series. The paddles in these forms were too small to have furnished much power in swimming, and the hind paddles were so reduced as to be practically functionless.

In a number of the species of *Ichthyosaurus* from the Lower Lias of England (fig. 48) the lower arches of the caudal series appear to be larger and extend out in the series to a point considerably beyond the bend in the tail. In these forms the area of the paddles is generally larger, and in many cases the posterior paddles are relatively large.

Among the Triassic ichthyosaurians the terminal portion of the caudal series is known in *Mixosaurus*, *Delphinosaurus*, and to a considerable extent in *Cymbospondylus*. Caudal vertebrae are also known from the other genera.

In *Mixosaurus* the well-preserved specimens at Milan show a structure which resembles that of *Ichthyosaurus* sufficiently to call to mind the type of tail fin present in the latter genus, but different enough to merit discussion as a distinct type (fig. 45). In this form the distal end of the caudal region was apparently not bent downward sharply as in the latest ichthyosaurs, but curved slightly upward near the middle of the caudal series and then down again some distance in front of the posterior end of the tail (fig. 50). This difference would not of itself attract attention so strongly were it not that the character of the vertebral arches in the flexed portion of the tail is very different from that in *Ichthyosaurus*. The neural arches instead of suffering gradual reduction as the point of curvature is approached, and disappearing very close behind it as in *Ichthyosaurus*, are considerably increased in length and stand erect in the curved region, and continue far back toward the terminal region of the series. In the Milan specimen best known to the writer the caudal region consists of about 76 vertebrae. The upper arches begin to turn forward at about the seventeenth centrum behind the posterior limb. The hypocentral elements are long, the inferior ends of the right and left pieces uniting to form Y-shaped arches. The writer has not seen lower arches immediately below the bend in the caudal series, but they are present and well developed behind the bend.

In a small specimen occurring in the same beds with *Cymbospondylus* in the Middle Trias of Nevada (no. 10624, fig. 44) prac-

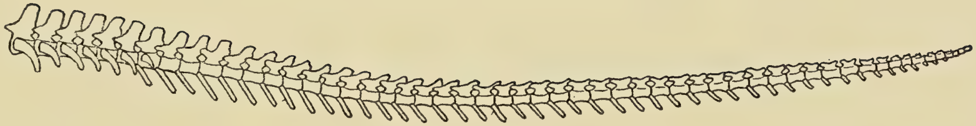


FIG. 43. *Palaeohatteria longicaudata* Credner. Caudal series, $\times \frac{1}{2}$. (Adapted from Osborn.)

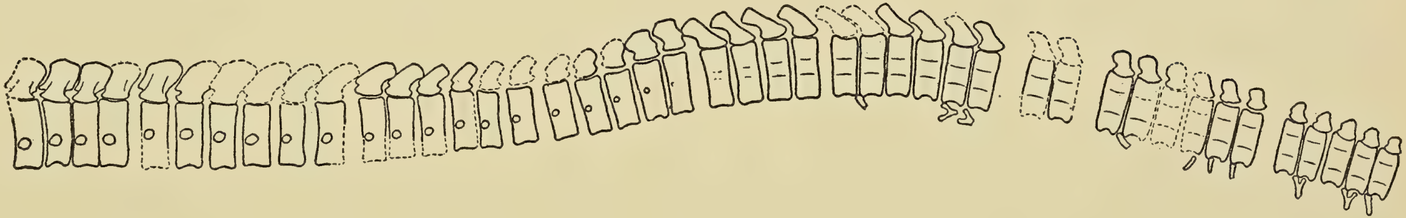


FIG. 46. *Cymbospondylus petrinus* Leidy. Caudal series, $\times \frac{1}{15}$.

tically the same relations of the elements of the caudal vertebrae appear as are found in *Mixosaurus*. The caudal centra are somewhat flattened laterally and bear apophyses, with which caudal ribs may have been in articulation. The neural arches are high and slender, their height equaling a little less than three times the height of the centra (× 2⅔). They show little if any anteroposterior curvature and stand nearly erect on the centra. The inferior arches are also long and slender, but are strongly recurved. Their length equals nearly two and one-half times the height of the centra. The articulation of each of the inferior arches seems to be mainly on a single centrum, instead of intervertebral. The union of the lower arches with the centra is so close that it may possibly amount to co-ossification in some cases.

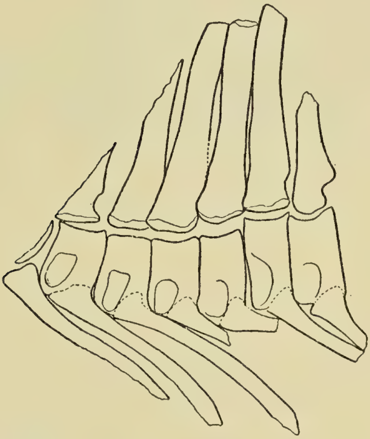


FIG. 44. *Cymbospondylus* (?) *natans* Merriam. Section of caudal fin, ×⅓.

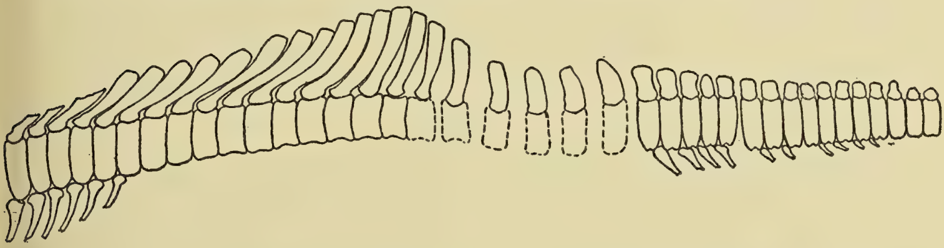


FIG. 45. *Mixosaurus cornalianus* (Bassani). Caudal series, × ½. (After Repossi.)

In a large specimen of *Cymbospondylus petrinus* (no. 9947, fig. 46) there is a continuous series of over fifty vertebrae showing the structure of the greater portion of the caudal region. At the thirty-fifth centrum in this series, which appears to represent a point normally thirty-five to forty centra behind the pelvis, a bend occurs in the tail. At this point the neural spines suddenly stand erect instead of inclining backward, and behind the thirty-fifth vertebra as far as the fifty-sixth they are inclined forward. The spines are not greatly elongated as in *Mixosaurus*, but keep a more nearly even height through the tail. At the thirty-fifth vertebra a change also occurs in the centra, which are considerably shortened inferiorly, indicating vertical curvature, and the diapophyses suddenly disappear. For some distance behind the thirty-fifth vertebra the centra increase somewhat in height and at the same time become absolutely narrower transversely. Small Y-shaped chevrons are present to the end of the series.

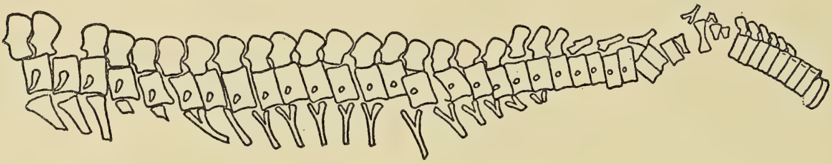


Fig. 47. *Delphinosaurus perrini* Merriam. Caudal series, × $\frac{1}{8}$.

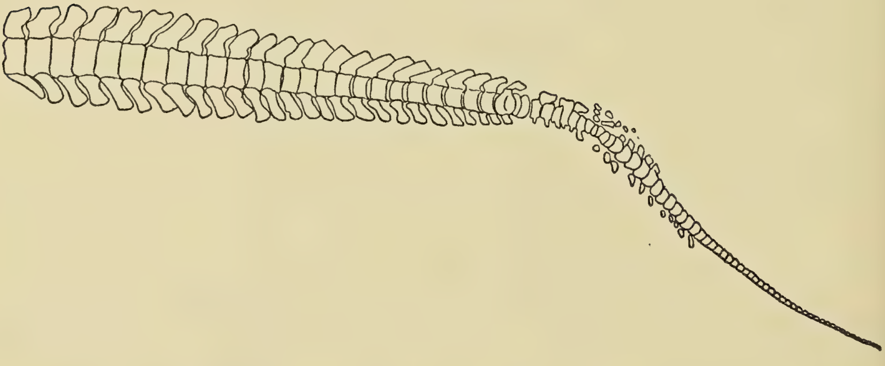


Fig. 48. *Ichthyosaurus intermedius* Conybeare. Caudal series, × $\frac{3}{16}$. (Adapted from Owen.)

In *Delphinosaurus* the caudal series shows a downward curve in the distal region not unlike that in *Ichthyosaurus*, though the bend is probably not so pronounced (fig. 47). The vertebral centra beyond the bend are small, but show some lateral compression, and are slightly higher than the centra immediately in front of the bend. Anterior to the bend in the tail the lower arches appear as long-spined chevrons. The chevrons are not certainly known behind the anterior region of the bend, but may have been present there. The upper arches of the centra in the anterior and middle region of the tail are of moderate height and are much flattened laterally. Immediately behind the bend the small upper arches turn sharply forward as in *Geosaurus* (fig. 52).

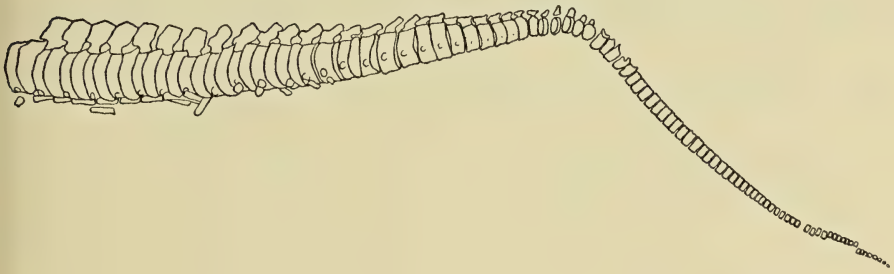


Fig. 49. *Ichthyosaurus quadriscissus* Quenstedt. Caudal series, about $\frac{1}{10}$ natural size. (After Fraas.)

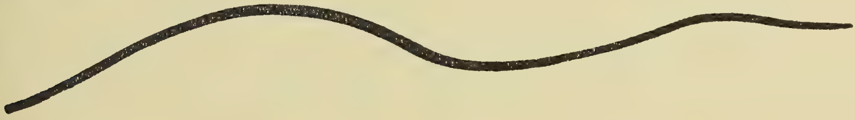


Fig. 50. Outline of the vertebral column of *Mixosaurus*. From rough sketch by the author.

The form of the caudal fin seen in *Mixosaurus* differs from that in *Ichthyosaurus* fundamentally in that the vertical expansion of the fin is produced in a large part by the elongation and erect position of the vertebral arches, whereas in *Ichthyosaurus* the arches have little or nothing to do with the widening of the fin. Sculling organs of a character somewhat similar to that of *Mixosaurus* appear in other groups, particularly in the mosasaurian genus *Clidastes* (fig. 51), in which a portion of the caudal region somewhat in advance of the posterior end of the series is considerably broadened by the elongation and erection of the neural arches. The inferior spines are also somewhat elongated, and although fused to individual vertebral centra they are quite strongly recurved.

The modification of the caudal fin of *Clidastes* differs from that of *Mixosaurus* mainly in showing less evidence of vertical curvature of the distal portion of the vertebral column. If the tail fin of *Cymbospondylus* (?) *natans* were better known it would possibly be found to differ from *Clidastes* in general character less than does the corresponding region in the caudal series of *Mixosaurus*.

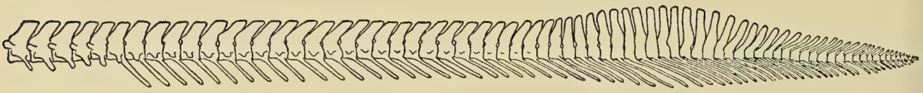


FIG. 51. *Clidastes velox* Marsh. Caudal series, × $\frac{1}{12}$. (After Williston.)

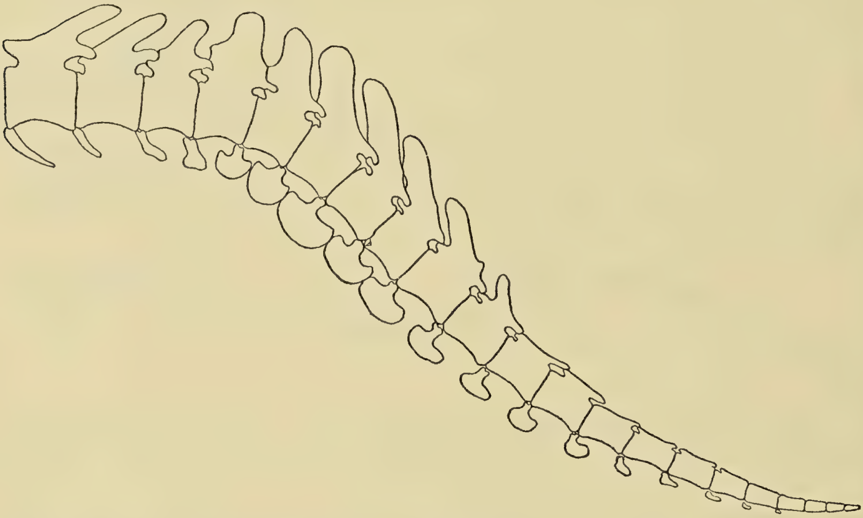


FIG. 52. *Geosaurus suevicus* E. Fraas. Caudal series, × $\frac{1}{2}$. (After Fraas.)

In the caudal fin of the typical *Cymbospondylus* the centra become higher and narrower beyond the bend, instead of smaller as in later forms, while the upper and lower arches are retained beyond the bend. The upper arches are inclined forward as in *Mixosaurus*, but are not extraordinarily elongated as in that genus and in *C.* (?) *natans*. Vertical expansion of the fin is produced in this instance partly by retention of the upper and lower arches, partly by increased height of the vertebral centra, and partly by vertical curvature of the column.

In the known history of the Ichthyosauria the caudal fin has passed through several fairly definite stages of evolution, and the trend of modification has always been in practically the same direction. The most primitive structure is probably that of *C.* (*?*) *natans* which leads to the type of *Mixosaurus*. In the large *Cymbospondylus* the structure is almost as primitive as in the other two Middle Triassic forms, the differences being possibly due in part to difference in size of the individuals compared.

Arranged in accordance with the hypothetical scheme of evolution of the ichthyosaurian caudal fin, the various known stages in the evolutionary series are, as shown below, also arranged in the order of their appearance in time; excepting in the case of those Middle Triassic forms in which the factor of size is also to be considered. In the case of these Middle Triassic forms size has exerted the influence which could generally be predicted, the smaller forms showing the most primitive structure.

The fact that the known forms fall into a fairly definite series is not necessarily to be taken as indicating a single direct line of descent. They are widely scattered geographically, and differ sufficiently in minor details of structure to make difficult their arrangement in a single series. The fact that wherever the forms of a given period are found they seem to fall into this predicted position in the evolutionary scheme indicates all the more clearly the definite and long-continued tendency of evolution of the group in this particular.

Including the hypothetical ancestors of the Ichthyosauria the following series of forms may be taken to represent stages in the evolution of the caudal fin:

1. Unknown littoral or terrestrial Permian ancestor with caudal series much as in *Palaeohatteria*; tail long, slender, not markedly expanded vertically, upper and lower arches imperfectly developed in posterior part of caudal series.

2. Unknown semiaquatic Permian or early Triassic ancestor. Caudal series long, tail considerably expanded vertically as in Crocodilia, upper and lower arches well developed excepting in terminal third or quarter of tail.

3. Early Triassic ancestor. Caudal series long, tail expanded vertically somewhat in advance of the posterior end by elongation

or erection of the arches. Possibly represented by *Cymbospondylus* (*?*) *natans* or a closely allied form.

4. *Mixosaurus.* Middle or Upper Triassic form with distal expansion of caudal region caused in part by elevation of the vertebral arches, and in part by vertical curvature of the vertebral column.

5. *Cymbospondylus.* Large Middle Triassic forms possibly represented by preceding stages in the young animal. Distal portion of caudal region retaining short Y-shaped chevrons, and short erected neural arches; vertebral centra increased in height and laterally compressed behind the bend.

6. *Delphinosaurus.* Upper Triassic. Expansion of the distal portion of the caudal fin due largely to curvature of the vertebral column. Upper and lower arches considerably reduced in the region of the caudal flexure. Anterior caudal region relatively broad owing to the presence of laterally compressed upper arches of moderate size, and of long-spined chevrons.

7. *Ichthyosaurus.* Lower Lias. Much as in *Delphinosaurus*, but lower arches shortened and no longer united ventrally.

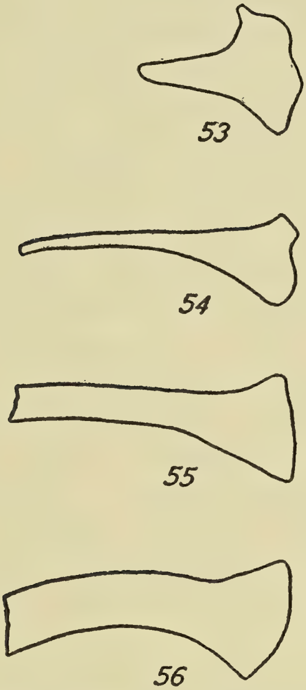
8. *Ichthyosaurus.* Upper Lias. As in Lower Lias, but with occasional almost complete reduction of lower arches.

9. *Ichthyosaurus*, *Ophthalmosaurus*, and *Baptanodon.* Upper Jurassic and Cretaceous. Lower arches much reduced or absent, anterior and posterior margins of vertebrae behind the bend swollen, and with articulation faces swinging outward and somewhat backward on the swollen tracts. Centra behind the bend in the tail suddenly reduced in size. (In *I. posthumus* they become relatively small and long.) Posterior portion of caudal series more strongly deflexed than generally in preceding forms.

As has perhaps been evident in the preceding statement of the evolution of the ichthyosaurian caudal fin, the historical series of forms which is now available suggests that the peculiar upper lobe of the ichthyosaur fin originated at that period in the history of the group when the height of the tail was increased by elongation of the neural arches, and that once having taken on an important function it has been retained and enlarged.

Ribs

In the Triassic ichthyosaurians, as in the typical *Ichthyosaurus*, rib articulations are present from the anterior cervical region along the whole of the vertebral column well out toward the distal region of the caudal series. Excepting the character of the rib articulation in certain regions, the general form of the ribs in the Triassic ichthyosaurs is not materially different from that in the later genera. The shaft is generally considerably flattened, excepting at the distal end, where it may be nearly round in cross-section. In all excepting the most anterior and posterior ribs the anterior and posterior sides of the shaft are more or less deeply grooved. Compared with *Ichthyosaurus*, the shaft is possibly somewhat shorter in the middle dorsal region of *Cymbospondylus* (pl. 7, fig. 1) and somewhat heavier in the dorsal region of some species of *Shastasaurus*.



FIGS. 53–56. *Cymbospondylus petrinus* Leidy. Rib series, $\times \frac{1}{3}$. Fig. 53, anterior cervical rib; fig. 54, posterior cervical rib; fig. 55, anterior dorsal rib; fig. 56, middle dorsal rib.

In all of the American Triassic ichthyosaurs, excepting *Toretocnemus*, the ribs articulate on the vertebral centra and arches, with a single head excepting in the most anterior portion of the column (figs. 53–56).

In the best known specimen of *Shastasaurus* showing the vertebral column (fig. 57) the centra of the anterior cervical vertebrae show both diapophyses and parapophyses. The parapophyses are situated low down on the centra and are somewhat less than half the size of the diapophyses. In passing back toward the anterior dorsal region the diapophyses are seen to grow longer, while the parapophyses become much reduced. The distance separating the two apophyses remains nearly the same, or is at least not decreased. On the twelfth centrum of the series the parapophysis is a mere tubercle without an articular face. The last trace is seen on the eighteenth centrum, on which a rudimentary tubercle is present on one side only. Beyond the point of disappearance of the parapophyses, the diapophyses continue to increase in length but no division of the rib articulation appears.

In the older genus *Cymbospondylus* much the same relations of the rib articulation are seen, and the parapophyses are gradually reduced in passing back through the cervical series until they disappear entirely in the posterior cervical or anterior dorsal region. In one specimen (fig. 58) the parapophyses retain nearly the same size from the axis to the twelfth centrum. On the thirteenth the diapophyses are suddenly elongated, and there is no parapophysis on one side, though a rudiment is present on the other side. The diapophyses have a peculiar form on this centrum, the lower ends being turned backward instead of forward.

In *Delphinosaurus* the same relation obtains as in *Shastasaurus*, and in *Merriamia* we know only that the middle dorsal ribs are single-headed.

In *Toretocnemus* (fig. 59) the middle and posterior dorsal ribs have deeply notched or forked heads articulating on distinctly separated diapophyses and parapophyses. The vertebrae and ribs of the anterior region of the column are unknown.

In the European *Mixosaurus* the rib articulations are said to be unicipital excepting a possible faint division in the posterior dorsal and anterior caudal region (figs. 60*a* and 60*b*).

In *Mixosaurus* (?) *atavus* of the European Muschelkalk the only anterior dorsal vertebra known (fig. 61) seems to have a double-headed rib articulation. Several posterior dorsals from the collections at Stuttgart (fig. 63) and Zürich have distinctly separated diapophyses and parapophyses low down on the sides of the centra.

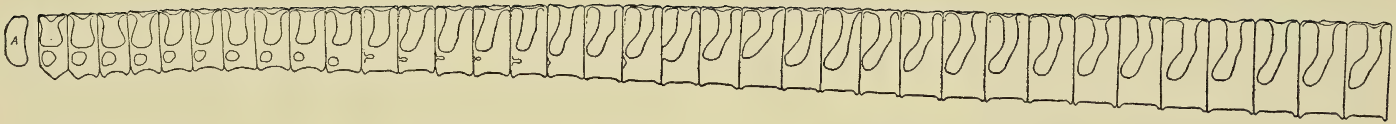


Fig. 57. *Shastasaurus osmonti* Merriam. Vertebral series of the type specimen, × ⅙. *A*, atlas restored from another specimen.

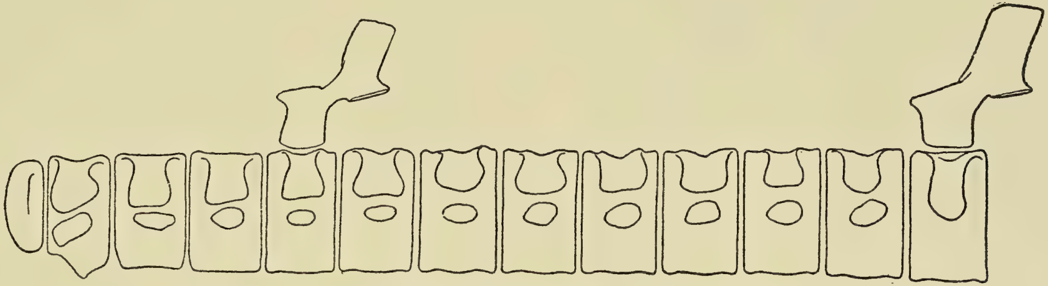


Fig. 58. *Cymbospondylus petrinus* Leidy. Vertebral series, × ⅕.

Other centra (figs. 64*a* and 64*b*) not far from the region of the pelvis have a single, large, lateral apophysis in which there may be some indication of narrowing near the middle. These last centra show no traces of facets for intercentra, and if located behind the pelvis could not be situated very far from it.

There are no vertebral centra available which certainly represent the middle dorsal region of *M.* (?) *atavus* unless some of those which have been referred to the anterior and posterior portions belong here. A peculiar centrum figured by Fraas (fig. 62) shows a cross-section similar to that of a middle dorsal, and possesses a small but prominent apophysis a little above the middle of each side. The writer has not seen so small an apophysis for unicipital articulation of middle dorsal ribs in any ichthyosaurs, but apophyses of this size, form, and situation occur in the middle caudal region.

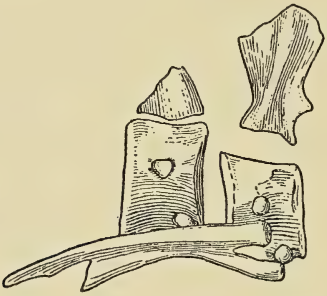
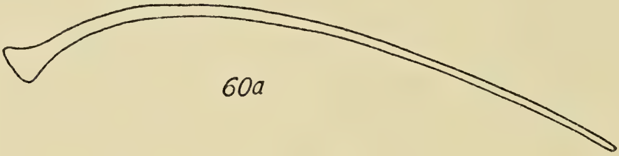
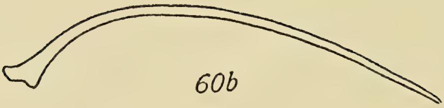


Fig. 59. *Toretocnemus californicus* Merriam. Vertebrae and rib from middle dorsal region, natural size.

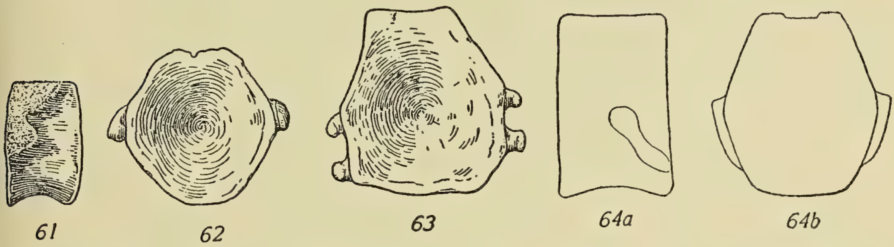




Figs. 60*a* and 60*b*. *Mixosaurus cornalianus* (Bassani). Ribs natural size. (After Repossi.) Fig. 60*a*, dorsal rib; fig. 60*b*, posterior or anterior dorsal rib.

The centrum shows a central perforation. Such perforations appear to be more common in the caudal centra than in other regions of the column, but the nearly circular cross-section is not characteristic of the caudal region. If the centrum is an anterior dorsal the apophysis present is possibly the parapophysis, the tubercle having rested on the base of the upper arch.

That forms of rib articulation as different as those discussed above for *M.* (?) *atavus* occurred in the same region of the vertebral column in variations of the same species or even of the same genus seems improbable. It would therefore appear that we are dealing either with different parts of the vertebral column of similar individuals, or with quite different generic or specific types occurring together, as do *Toretocnemus* and *Merriamia* in the Upper Triassic of California. Apparently the only other possible situation in which either of the types of vertebrae referred to the posterior dorsal region could be placed would be the anterior caudal region; and that either form could be referred to this series is improbable as chevron facets are not present, and all other Triassic forms as well as most Jurassic ichthyosaurs possess well developed caudal hypocentra.



Figs. 61–64*b*. *Mixosaurus* (?) *atavus* (Quenstedt). Vertebrae × $\frac{4}{5}$. Fig. 61, anterior dorsal or posterior cervical; fig. 62, middle caudal or middle dorsal; fig. 63, posterior dorsal; figs. 64*a* and 64*b*, from posterior dorsal or most anterior caudal region; figs. 61, 64*a* and 64*b*, from rough sketches by the author; figs. 62 and 63, after Fraas; figs. 61–63, from specimens in the König. Naturalien-Cabinet, Stuttgart; figs. 64*a* and 64*b*, from a specimen in the Polytechnikum, Zürich.

In the case of *Mixosaurus*, in which a division of the rib heads is supposed to occur in the caudal region, Yakowlew (1902, 2) has suggested that the rib articulations were originally single-headed, and that a division into two heads began in the caudal region owing to the influence of the peculiarly powerful lateral movements of the tail in swimming. Having in mind the desirability of determining the nature of the rib articulations in the pelvic region of *Mixosaurus*, the writer has examined a number of the excellent specimens at Milan. This examination shows that in some cases, at least, the short ribs near the pelvic region or the base of the tail have broad, undivided heads as in the shastasaurian forms of the American Trias. In other instances ribs belonging to the anterior caudal region seemed actually to show a beginning division of the articular face. In one case, where the evidence seemed strongest, the apophysis on the vertebral centrum showed also some indication of division. It should, however, be noted that even in this instance the evidence hardly warrants a definite statement that double articulation occurs, as the side of the vertebral centrum is badly broken up, and does not present a satisfactory surface on which to make a thoroughly trustworthy observation. The heads of these ribs are moreover not fully exposed, and it is not impossible that further preparation with a needle will show that the apparent gap between the head and tubercle is filled by a bridge of bone covered by matrix lying in the extension of a lateral groove. It is also worth noting that ribs with heads formed as these appear to be as they are shown in the matrix could not come into direct articulation with the diapophysis without elevating the shaft above the level of the other ribs.

In the case of the American Triassic genera, careful search has been made to determine whether any division of rib heads in the posterior dorsal or caudal region could be discovered in any type excepting *Toretocnemus*. In the posterior dorsal region the rib heads are found to be generally very broad, but show no indication of incipient division. In the caudal ribs no evidence of division of the head has been observed.

From the evidence available, some doubt must exist as to the true character of the rib articulation in the ancestral ichthyosaur. In all Triassic types excepting *Toretocnemus* and certain forms of the *M.* (*?*) *atavus* group the articulation is predominatingly unicipital. In all post-Triassic forms the articulation is mainly bicipital. If the double-headed articulation is primitive, such forms as *Cymbospondylus*, *Mixosaurus*, *Delphinosaurus*, and *Shastasaurus* are presumably not in the direct line of descent, and the later ichthyosaurs are probably to be derived from some such form as *M.* (*?*)

atavus or *Toretocnemus.* If the unicipital articulation is primitive either *Cymbospondylus* or *Mixosaurus* might stand near the line of descent.

As far as the known relationships of the Ichthyosauria are concerned, there seem to be no particularly strong reasons for considering that either of the known types of articulation must be the primitive one. Single-headed ribs are perhaps the rule in the primitive Diaptosauria, but incipient bicipital articulation seems to be present in *Kadaliosaurus.* In the Phytosauria, which have been considered as probably very closely related to the Ichthyosauria, the rib articulation is markedly double-headed in the cervical and dorsal regions. If the ancestry of the ichthyosaurian group be pushed back far enough so that its origin may be considered to represent as early a date as that of the Diaptosauria, the ichthyosaurs must be supposed to have originated from some branch not far from the original cotylosaurian stem.

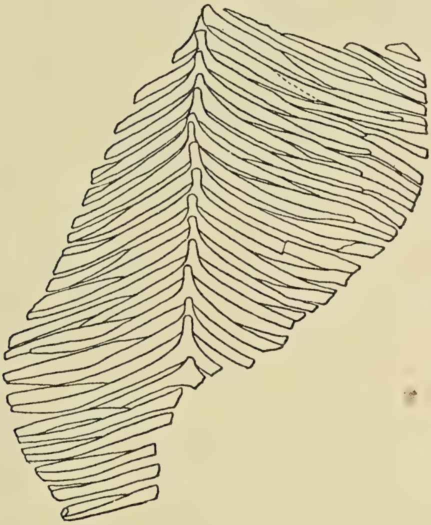


Fig. 65. *Cymbospondylus petrinus* Leidy. Abdominal rib plastron, × $\frac{3}{20}$.

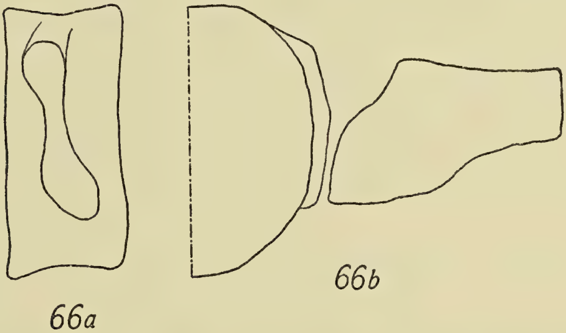
Excepting *Toretocnemus*, some of the *M.* (?) *atavus* specimens, and a doubtful division of the posterior dorsal and anterior caudal rib heads in *Mixosaurus*, double-headed articulation in the Triassic forms is limited to the most anterior region of the column, and in this region it becomes less pronounced in passing back from the most anterior cervicals. In the region of the thorax, where the ribs are long and are particularly influenced by the movements of the lungs, they have a single head. The Ichthyosauria being purely aquatic, high-sea animals may have remained under water for a considerable period at times, and have required a large intake of air before submergence, and full inspiration on returning to the surface. In the Cetacea, living under somewhat similar conditions, we find the most specialized forms showing a tendency to reduce the rib articulation of the dorsal region to a single head. This head is in the cetaceans, as in the shastasaurian ichthyosaurs, the upper head or the one allowing the widest excursion of the ribs in inspiration. In the Cetacea it may be noticed also that the reduction of the lower rib heads takes place progressively forward, or occurs last in the most anterior ribs, as in *Shastasaurus*. In the shastasaurs a number of distinctly double-headed ribs have remained in the anterior region of the column. In the whales there being no cervical ribs the double articulation may show an apparently more extreme reduction.

In the Cetacea where the capitulum has become reduced, the tuberculum is usually only loosely attached, allowing the greatest possible movement. In *Shastasaurus* the single rib articulation of the dorsal region is marked by the development of an angle or prominence on the rib head and on the diapophysis. The articulations are so situated on both faces that the upper portion of the rib head and diapophysis turn away from each other, leaving a gap which was evidently partly filled in with cartilage or connective tissue (fig. 66). The cutting out of space between the upper portion of the rib and the diapophysis permitted a rocking movement of the rib head of such a nature as to allow extraordinary elevation of the distal end of the rib shaft, and without reducing the head to abnormally small dimensions.

A careful examination of the vertebral rib articulation in the cervical and anterior dorsal regions of *Shastasaurus* and of most specimens of *Cymbospondylus* suggests most strongly that in passing backward through the series the parapophysis is gradually disappearing, and the articulation is becoming solely tubercular or diapophysial. Yakowlew (1902, 1) has suggested that the bicipital articulation in Ichthyosauria has arisen through the splitting of single-headed ribs, or by atrophy of the median region of the head.

If, however, the double-headed rib is derived from a single-headed form by reduction of the middle portion of the head, the reduction would probably not begin, as it does in the anterior dorsal region of *Shastasaurus*, by separation of a small and apparently functionless tubercle some distance away from the main rib head (fig. 57). The division would occur according to this method by gradual constriction of the rib head until a small space came to exist between two large and functional heads. Though such a condition occurs in other reptilian groups, it has not thus far been known to exist in the Triassic Ichthyosauria.

In *Shastasaurus* and *Cymbospondylus* the parapophyses generally remain about the same distance from the diapophysis no matter how large they are. Though the diapophysis gradually increases in height, the lower border never meets the parapophysis. In passing backward through the series the diapophyses gradually increase in size and the parapophyses decrease in size till the latter disappear, but at the point of disappearance the parapophyses are not absorbed into the diapophyses. The only case which might be considered as an exception to this rule is that of a specimen of *Cymbospondylus* (fig. 58) in which large parapophyses are present back to the twelfth centrum. On the thirteenth centrum the diapophyses are much increased in size, while the parapophysis has disappeared on one side and is represented only by a rudiment on the other side. The diapophyses on the thirteenth centrum are



FIGS. 66*a* and 66*b*. *Shastasaurus altispinus* Merriam. Middle dorsal vertebra and rib, illustrating rib articulation, × ⅓. Fig. 66*a*, lateral view of centrum; fig. 66*b*, anteroposterior profile of centrum and rib.

also of a peculiar form, being swung backward instead of forward. The parapophyses do not gradually approach the diapophyses on this specimen but are separated from them by a nearly uniform space.

If the double articulation has arisen from a single articulation in the forms described above it must have come in most cases through addition of an entirely independent rib head, and an inferior or parapophysial tubercle. This would mean that in the case of the rudimentary structures in the anterior dorsal region, both parapophysis and lower rib head appeared and developed to a considerable size before they could have any important function; and that the local conditions requiring a lower tubercle have progressed from the anterior cervical to the anterior dorsal region in *Shastasaurus*, or to the posterior dorsal region in *Ichthyosaurus* and *Baptanodon*.

In view of what has been said above, it seems less probable that the double articulation in the anterior dorsal region of the Shastasaurinae is incipient than that it is rudimentary; and it is possibly in order to consider the forms exhibiting this type of rib articulation as a side branch of the Ichthyosauria, which early developed a tendency to reduce the dorsal ribs to a single head.

Abdominal Rib Plastron

Elements of the abdominal rib plastron are known with nearly all of the Triassic forms, but are in most cases scattered or disturbed to such an extent that their arrangement cannot be clearly determined. In one specimen of *Cymbospondylus petrinus* a portion of the rib plastron shown in fig. 65 was preserved without displacement of the elements. Each transverse series consists of a broadly V-shaped median piece and two lateral pieces. The median element is not divided into two parts as in some forms of *Ichthyosaurus*, but is produced forward as a prominent knob at the point of union of the lateral arms. All of the elements of the plastron seem to be heavier and more robust than in *Ichthyosaurus*. On this specimen there seem to be two transverse series of abdominal ribs for each pair of true ribs.

In *Mixosaurus* the nature of the abdominal ribs is, according to Repossi's figures (Repossi, 1902, tav. 8, fig. 1, and tav. 9, fig. 1), much as in *Cymbospondylus*, excepting that the elements are possibly less robust, and the anterior projection of the median pieces is acuminate, and is longer.

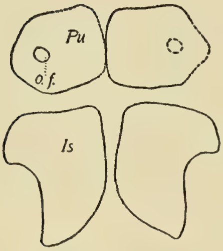
Limb Arches

The Triassic Ichthyosauria differ generally from the later types in the closer agreement in size of the corresponding elements in the two limb arches. Though there are some notable exceptions, as in *Mixosaurus* and *Merriamia*, the anterior and posterior limbs, and consequently the pectoral and pelvic arches do not differ as widely in size as they are commonly seen to do in *Ichthyosaurus* and the later genera. A second difference generally distinguishing the arches of the earlier forms is found in the greater expansion of most of the elements, particularly of the pelvic arch. The large size and more robust character of the elements of the pelvic girdle are to be interpreted as directly indicating greater efficiency of the posterior limbs. The greater strength of the hind limbs probably indicates less effectiveness in the caudal fin. The anterior arch as a whole is heavy, but is not stronger than the arch of some forms of *Ichthyosaurus*.

Pelvic Arch.—In most cases the elements of the pelvis differ so far from the corresponding bones of post-Triassic forms that they might readily be considered as representing a quite different reptilian group. This is particularly true of the two inferior elements, which are much broadened, and show the expanded plate-like form seen in some of the most primitive reptilian types.

The ilium as known in *Toretocnemus* (fig. 69) appears to be considerably elongated and is relatively slender. In *Cymbospondylus* (fig. 70) the ilium is somewhat shorter and is considerably expanded distally. As seen in specimen 9950, in which the elements of the pelvic arch seem to have held together, the ilium is turned forward at the proximal end. Nearly the same form of ilium is present in *Delphinosaurus* (fig. 72) and *Shastasaurus* (fig. 73). In *Delphinosaurus* there is on the posterior side, near the proximal end, a small tubercle which does not appear in any of the other forms, and reminds one of the anterior extension of the upper portion of the ilium in land or shore forms with a strong sacral attachment.

All of the Triassic genera agree in the broad expansion of the distal portion of the pubis, but there is among them a considerable variation in the form of the proximal end of the bone. According to Repossi (1902, tav. 9, fig. 3), in *Mixosaurus* (fig. 71) the strongly curved median margin of the pubis bends into the proximal end of the bone without the formation of a hook and there appears to be no opening corresponding to the obturator foramen. In *Toretocnemus* the pubis is very broad proximally as well as distally, and is perforated by an obturator foramen. In *Cymbospondylus* an obturator foramen may be present as in *Toretocnemus*. In some cases the opening may possibly be incompletely surrounded by a broad, recurved hook formed by the much expanded median side of the blade as in *Shastasaurus*. In *Delphinosaurus* and *Shastasaurus* the pubis is much expanded distally, and the expanded middle portion curves backward so as to form a very prominent hook.



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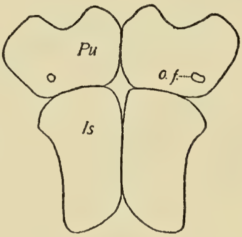

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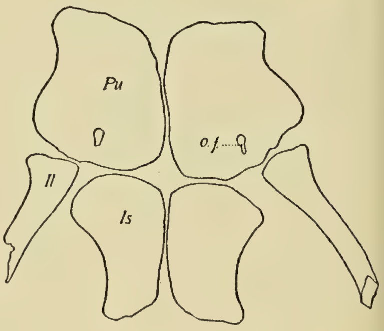

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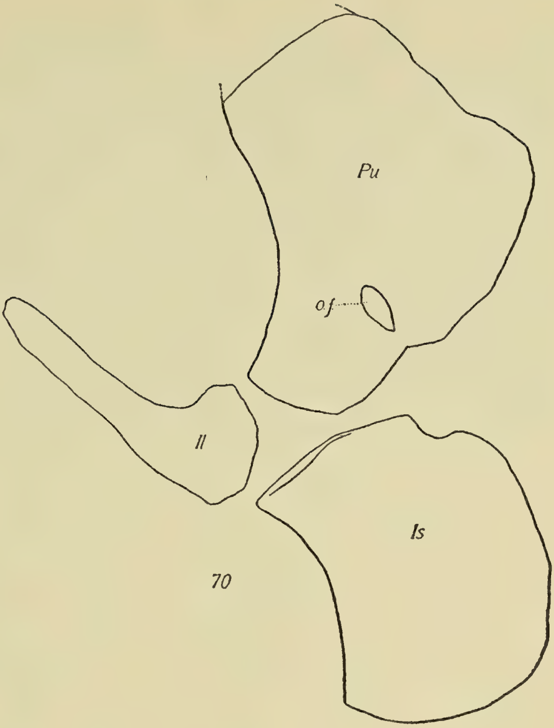
FIG. 67. *Procolophon trigoniceps* Owen. Pelvis, × ⅘. (After Broom.) *Pu*, pubis; *Is*, ischium; *O.f.*, obturator foramen.

FIG. 68. *Stereosternum tumidum* Cope. Pelvis, × ⅘. (After Osborn.) *Pu*, pubis. *Is*, ischium; *O.f.*, obturator foramen.

FIG. 69. *Toretocnemus californicus* Merriam. Pelvis, × ⅘. *Pu*, pubis; *Is*, ischium; *Il*, ilium; *O.f.*, obturator foramen.

The form of the ischium is less variable than that of the other elements. In all cases it is an expanded plate-like element without distinctly marked tuberosities or constrictions. It shows the greatest transverse expansion in *Cymbospondylus*, in which in some instances the width almost equals the length (see fig. 134, p. 349). The narrowest form is seen in *Toretocnemus*, though the expansion is considerable even in that genus.

The character of the pelvis in the Triassic Ichthyosauria much



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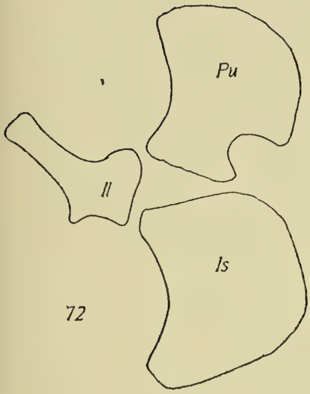

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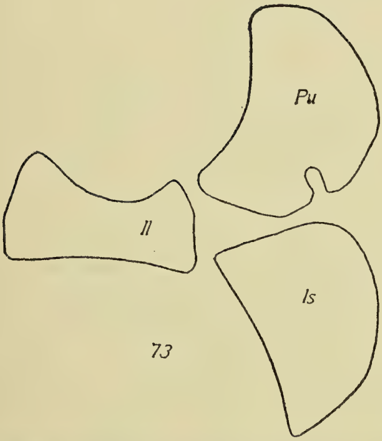

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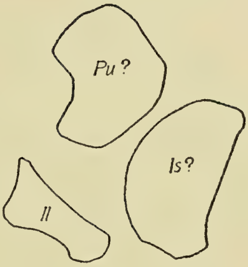

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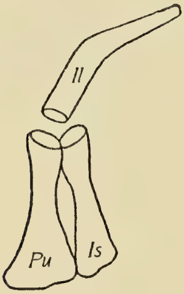
FIG. 70. *Cymbospondylus petrinus* Leidy. Pelvis, $\times \frac{1}{5}$. *Pu*, pubis; *Is*, ischium; *Il*, ilium; *O.f.*, obturator foramen.

FIG. 71. *Mixosaurus cornalianus* (Bassani). Pelvis, $\times \frac{9}{10}$. (After Repossi.) *Il*, ilium; *Pu?*, pubis?; *Is?*, ischium?.

FIG. 72. *Delphinosaurus perrini* Merriam. Pelvis, $\times \frac{9}{20}$. *Pu*, pubis; *Is*, ischium; *Il*, ilium.

FIG. 73. *Shastasaurus osmonti* Merriam. Pelvis, $\times \frac{9}{40}$. *Pu*, pubis; *Is*, ischium; *Il*, ilium.

resembles that of the early diaptosaurian reptiles particularly in the nature of the inferior or ischio-pubic portion. The upper portion of the ilium is less robust than in the Protorosauria and Pelycosauria, but not less so than in the Proganosauria, Choristodera, and Rhynchocephalia. The pubis and ischium of *Toretocnemus* resemble the corresponding bones of *Stereosternum* (fig. 68) in all but minor details of outline, and so far as can be determined the ilium is also similar. In *Procolophon* (fig. 67) the inferior elements are like those of *Toretocnemus*, though the form of the pubis is more nearly circular. In *Champsosaurus* the ischium is similar and the pubis is perforated by an obturator foramen. From the inferior elements of the arch in *Palaeohatteria*, *Toretocnemus*, and *Cymbospondylus* differ mainly in the presence of a closed obturator foramen instead of an obturator notch. Excepting *Toretocnemus* and *Cymbospondylus* all of the American Triassic genera resemble *Palaeohatteria* in the general form of the ischium, and in the development on the pubis of a posterio-median hook bordering an obturator notch. Of the known forms, *Mixosaurus* is the only one in which neither foramen nor notch appears in the pubis, though otherwise the form of the element here differs but little from that in the other genera.



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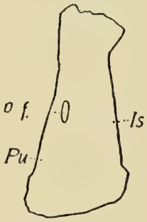

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FIG. 74. *Ichthyosaurus communis* Conybeare. Pelvis, × ⅓. *Pu*, pubis; *Is*, ischium; *Il.* ilium. (After Woodward.)

FIG. 75. *Ophthalmosaurus icenicus* Seeley. Ischio-pubic bone, about ⅙ natural size. *Pu*, pubis; *Is*, ischium; *O.f.*, obturator foramen. (After Andrews.)

As has previously been suggested by the writer (1902, 2, p. 86), though the pelvis of the Triassic Ichthyosauria shows some resemblance to that of the Plesiosauria, the form shown here denotes mainly a less complete accommodation of the skeleton as a whole to aquatic conditions than we find in the Jurassic ichthyosaurs. Koken[23] has seemed to imply that the plate-like pelvis of *Shastasaurus* is not primitive, but represents a peculiar accommodation.

The question as to what constitutes a primitive character is not always readily determined, but it would seem that in this case there could be no misunderstanding. The course of evolution of the Ichthyosauria has led quite definitely up to a form in which the principal motive power came to be exerted through the caudal fin, and as the tail became more powerful the hind limbs were reduced in size and strength until their function amounted almost to nothing. In all of the recognized divisions of the Ichthyosauria, even in the specialized Shastasaurinae, the tendency to development of a powerful sculling tail seems to have been the same, and the ultimate result of evolution if continued long enough must have been the reduction of the hind limbs. In the course of this reduction of the limbs, the arches have been reduced, until in the latest type the rudimentary ischium and pubis are fused. Inasmuch as evolution of the particular kind seen in the ichthyosaurs leads to great reduction or loss of the pelvis, a posterior arch in which the elements have approximately the form and relative size seen in the primitive reptiles, and are associated with a large limb, may well be said to be more primitive than that of *Ichthyosaurus.*

In the course of the reduction of the arch in the various divisions of the Ichthyosauria, it is to be expected that slightly varying forms would be assumed. That some of the variations which were in use while the posterior limb was large and functional might represent some slight phase of special adaptation is true, though the contention of the writer as previously expressed has not been that the pelvis itself was more primitive, but that it indicated less complete accommodation of the skeleton as a whole to purely aquatic conditions than we find in the Jurassic *Ichthyosaurus*. That the pelvis considered by itself might be assumed to be really more primitive than in the later Ichthyosauria appears also to be true, when we consider the extent to which the pelvic arches of all Triassic genera resemble the type of pelvis seen in most of the early Diaptosauria.

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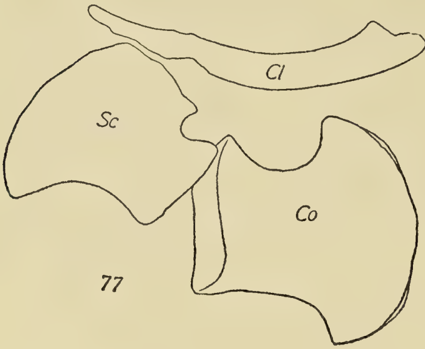
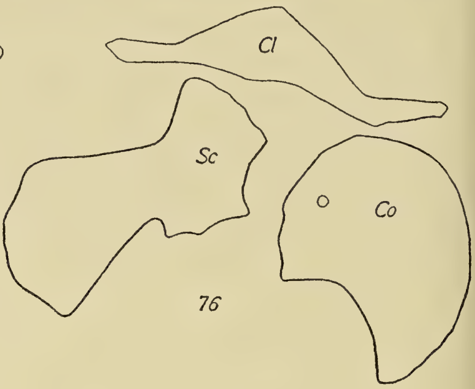
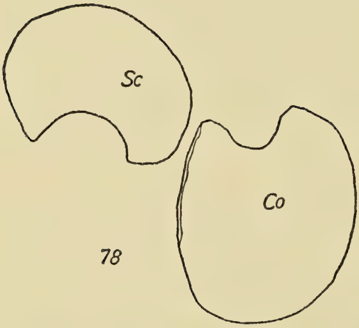
[23] Koken, E., N. Jahrb. f. Min. Geol. Palae., Bd. 1, p. 149, 1906.

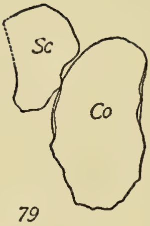
"Das Becken von *Ichthyosaurus* ist nicht eigentlich angepasst; es durchläuft eine Reihe von Veränderungen, welche seinen Funktions-wert mehr und mehr herabsetzen; gerade bei *Shastasaurus* liegt Anpassung vor, wie bei Plesiosauriern, weil wahrscheinlich, das geht aus den Resten der kräftigen Hinterextremität hervor, diese ein wichtiges Lokomotionsorgan blieb."

The view expressed by Koken is possibly not intended to be materially different from that of the writer as given above; though taken with the context it appears to be a criticism of the writer's suggestion that the form of the pelvis indicates "less complete accommodation of the shastasaurian skeleton to purely aquatic conditions than we find in the Jurassic *Ichthyosaurus.*"









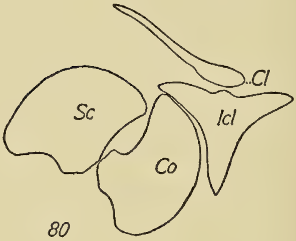


FIG. 76. *Cymbospondylus petrinus* Leidy. Pectoral arch, × $\frac{4}{25}$. *Sc*, scapula; *Co*, coracoid; *Cl*, clavicle.

FIG. 77. *Shastasaurus osmonti* Merriam. Pectoral arch, × $\frac{1}{5}$. *Sc*, scapula; *Co*, coracoid; *Cl*, clavicle.

FIG. 78. *Delphinosaurus perrini* Merriam. Pectoral arch, × $\frac{3}{25}$. *Sc*, scapula; *Co*, coracoid.

FIG. 79. *Merriamia zitteli* (Merriam). Pectoral arch, × $\frac{8}{25}$. *Sc*, scapula; *Co*, coracoid.

FIG. 80. *Mixosaurus cornalianus* (Bassani). Pectoral arch, × $\frac{8}{25}$. *Sc*, scapula; *Co*, coracoid; *Cl*, clavicle; *Icl*, interclavicle. (After Repossi.)

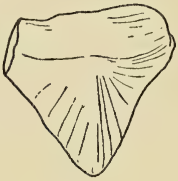
Pectoral Arch.—The shoulder girdles of the earlier ichthyosaurs resemble that of *Ichthyosaurus* in strength and compactness, but differ generally in the form of the individual elements. The only bone which is known to be constantly different is the scapula. This is always much expanded distally compared with the form in all post-Triassic species. The interclavicle, which is certainly known only from *Mixosaurus*, is nearly triangular, instead of T-shaped with a slender median stem as in the later genera. The coracoid and clavicle may resemble the corresponding bones in certain species of *Ichthyosaurus*, but are generally distinguished by features which are particularly characteristic of Triassic genera.

In *Mixosaurus* and *Shastasaurus* the coracoid is narrowed or pedunculate proximally, as in *Ichthyosaurus communis* and in the early Liassic species generally. In *Cymbospondylus* and *Delphinosaurus* it is broadly sickle-shaped, the *Cymbospondylus* type being distinguished by an anterior perforation. In *Merriamia* the coracoid is nearly elliptical without constriction or emargination, somewhat as in *Ichthyosaurus integer*. As far as has been determined, the natural groups into which the Ichthyosauria of the Triassic seem to fall do not show more uniformity in the character of the coracoid than is seen in the ichthyosaurian groups represented in the Jurassic. There is, however, a general tendency toward narrowing of the proximal portion much as is common in the forms of the Lower Lias.

The scapula in all known Triassic ichthyosaurs is relatively broad distally, and in most of the genera as *Mixosaurus*, *Shastasaurus*, and *Merriamia* the broad distal blade with an anterior hook shows considerable resemblance to the form seen in the Mosasauria. In *Delphinosaurus* the same form of distal expansion is seen, but the proximal region of the anterior margin is not cut out so as to produce an anterior hook. In *Cymbospondylus* the form of the element is more like that in *Ichthyosaurus*, though the distal end is very much broader and the proximal region of the anterior side is much enlarged.

The clavicle of *Cymbospondylus* appears to be considerably more expanded in the middle than in other forms. In *Mixosaurus* this element is rather slender excepting at the median end. The clavicle of *Shastasaurus* is slender.

It is rather remarkable that the interclavicle is not recognized on any American specimen representing the Triassic Ichthyosauria; excepting possibly the type of *Merriamia*, in which its form is not clearly shown. In *Mixosaurus* it is markedly broader than in the later forms, and might better be denominated triangular than T-shaped as in *Ichthyosaurus.* Von Huene (1902, p. 11) has described from the Wellenkalk near Calw a thick triangular bone which he recognizes as an ichthyosaurian episternum. Placed in series with the interclavicles of *Mixosaurus* and *Ichthyosaurus quadriscissus,* as has been done by von Huene (figs. 81–83), there appears a very marked shrinking of the originally triangular element to the three radii of the triangle in *Ichthyosaurus.*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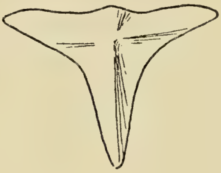
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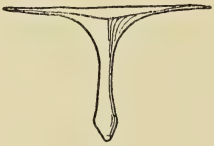
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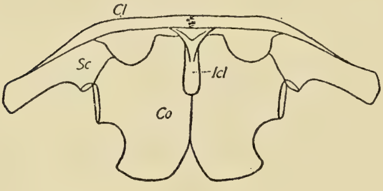
Fig. 81. *Mixosaurus* (?) *atavus* (Quenstedt). Interclavicle, $\times \frac{1}{2}$. (After von Huene.)
Fig. 82. *Mixosaurus cornalianus* (Bassani). Interclavicle, $\times \frac{1}{2}$. (After von Huene.)
Fig. 83. *Ichthyosaurus quadriscissus* Quenstedt. Interclavicle, $\times \frac{1}{2}$. (After von Huene.)



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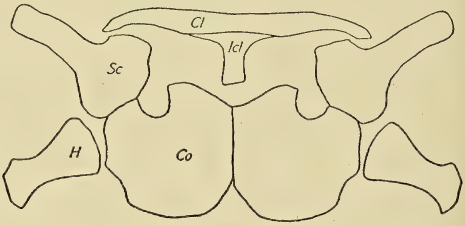

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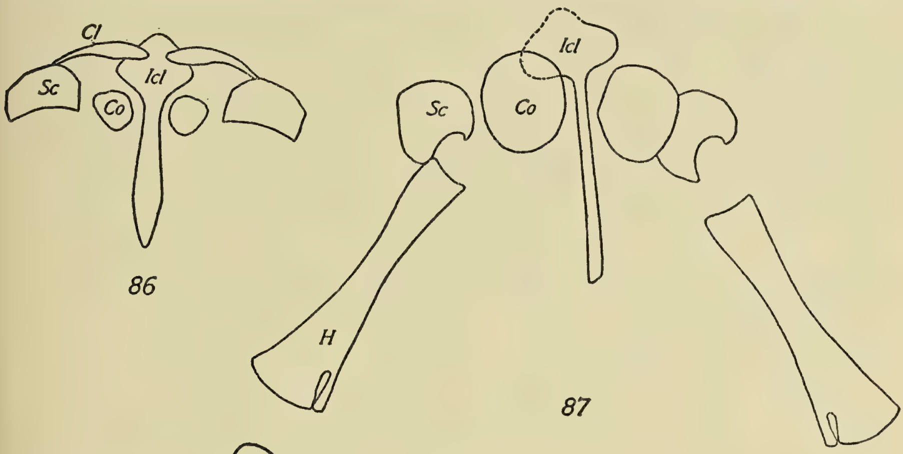
Fig. 84. *Ichthyosaurus communis* Conybeare. Pectoral arch, much reduced. *Sc,* scapula; *Co,* coracoid; *Cl,* clavicle; *Icl,* interclavicle. (After Woodward.)
Fig. 85. *Baptanodon discus* Marsh. Pectoral arch, $\times \frac{1}{13}$. *Sc,* scapula; *Co,* coracoid; *Cl,* clavicle; *Icl,* interclavicle; *H,* humerus. (After Gilmore.)

The shoulder girdle of the earliest known representatives in the Triassic was already considerably specialized in accommodation to the necessary functions of the fairly large paddles. The degree of specialization seen in this arch is probably greater than in the pelvis, inasmuch as the anterior limbs, being farther away from the caudal fin, interfere to a less extent with the movement of the tail, and have a more definite and permanent value in the swimming mechanism of the animal. It might therefore be considered at the outset as a more difficult matter to determine affinities by the use of these elements than by comparison of the bones of the pelvis.

Probably, for the reasons given above, the anterior arch of the Triassic ichthyosaurs does not show the degree of correspondence



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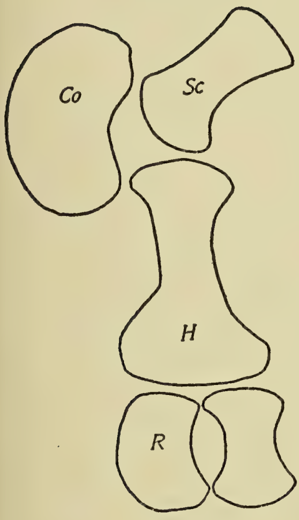

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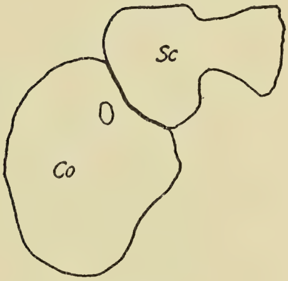

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FIG. 86. *Palaeohatteria.* Pectoral arch. *Sc*, scapula; *Co*, coracoid; *Cl*, clavicle; *Icl*, interclavicle. (After Credner.)

FIG. 87. *Stereosternum tumidum* Cope. Pectoral arch, × 2. *Sc*, scapula; *Co*, coracoid; *Icl*, interclavicle; *H*, humerus. (After Osborn.)

FIG. 88. *Thalattosaurus alexandrae* Merriam. Pectoral arch and limb, × $\frac{3}{8}$. *Sc*, scapula; *Co*, coracoid; *H*, humerus; *R*, radius.

FIG. 89. *Champsosaurus laramiensis* Brown. Pectoral arch, × $\frac{1}{2}$. *Sc*, scapula; *Co*, coracoid. (After Brown.)

with the pectoral girdle of early diaptosaurians that is generally evident in comparison of the posterior girdle with that of these forms. There is really no one of the diaptosaurian groups in which the correspondence is known to be as close in the anterior arch as it is in the posterior one. In *Stereosternum* (fig. 87) the anterior arch is not perfectly known, but the coracoid appears to be oval and imperforate in the young, and of somewhat similar form but perforate in the adult. The supposed scapulae of a young individual[24] are semi-lunar in form, and the interclavicle shows a diamond-shaped expansion at the anterior end of a long and slender shaft. In *Palaeohatteria* (fig. 86) the coracoids are small and discoidal, the interclavicle is closely similar to that of *Stereosternum*, and the scapula seems to differ mainly in the lack of excavation of the posterior border.

In comparison with the above forms the broadly triangular interclavicle of *Mixosaurus* suggests the expanded anterior end of this element in *Stereosternum* and *Palaeohatteria*, though the differences are considerable. The scapula of *Stereosternum* resembles that of *Delphinosaurus*, the broad perforated coracoid is a little like the perforated coracoid of *Cymbospondylus*, and the imperforate oval form corresponds to the type seen in *Merriamia*. There is no single ichthyosaurian form in which all of the characters of *Stereosternum* or of *Palaeohatteria* are seen. As near an approach to the form of the pectoral girdle of a Triassic ichthyosaur as is known is found in the Proganosauria. In *Champsosaurus* (fig. 89) the girdle is not markedly different from the anterior arch of *Cymbospondylus* so far as known. The scapula has nearly the same form lacking only some of the distal expansion seen in *Cymbospondylus*. The coracoid of *Champsosaurus* is perforated as in *Cymbospondylus*, but is more nearly elliptical, instead of sharply excavated on the postero-lateral border. The clavicles are large in both forms. The interclavicle of *Champsosaurus* is T-shaped as in *Ichthyosaurus*, but this element is unknown in *Cymbospondylus*.

The type of arch seen in the Triassic ichthyosaurs seems to approach most closely the form seen in the Diaptosauria, but owing to important changes in the functions of the anterior limb in adaptation to natation, it has come to vary considerably from that type in most cases.

[24] Osborn, H. F., Mem. Am. Mus., vol. I, p. 487.

Limbs

As early as the Triassic the amount of differentiation shown in the limb structure of the Ichthyosauria is surprisingly large, and apparently indicates that several fairly distinct lines of evolution or adaptation had been laid down. Excepting the greatly specialized shastasaurian species of the uppermost portion of the Upper Trias there is, however, in all of these varied forms an interesting group of characters which seem to interpret themselves only as persisting features of a primitive littoral ichthyosaurian with extremities having functions quite different from those of the true *Ichthyosaurus*.

In general the limbs of Triassic ichthyosaurians are distinguished by the following characters (see figs. 90–101): the epipodial elements are relatively long and are separated by a median space; in one or both of the epipodials there is a tendency to show a median constriction; the phalangeal region of the limb is relatively short; hyperdactyly never occurs; hyperphalangy is much less pronounced than in the later forms; the individual phalanges are relatively long, they are commonly notched on one or both borders even in the digits not situated on the borders of the limb, and may in many cases show a median constriction or shaft portion. Though it is not true of several of the genera, the hind limbs are generally relatively large. In *Toretocnemus* they appear to be fully as large as the anterior limbs. In *Cymbospondylus* and *Shastasaurus* they seem to have been almost as large.

While most of the above characters appear together in nearly all of the known Triassic forms, there have been developed in the Triassic some limb specializations which have eliminated certain of the primitive characters just mentioned. This is particularly true of *Shastasaurus*, which is, however, a very late Triassic form, and also represents a peculiar line of limb specialization apparently not present in the Jurassic genera.

As nearly as can be determined, at least two types of limb structure are represented in the Triassic genera. One form is seen in the broad paddle of *Mixosaurus* with a long podial[25] region, four proximal mesopodials, an alternating arrangement of the first and second rows of mesopodials, and five digits. A second form is seen

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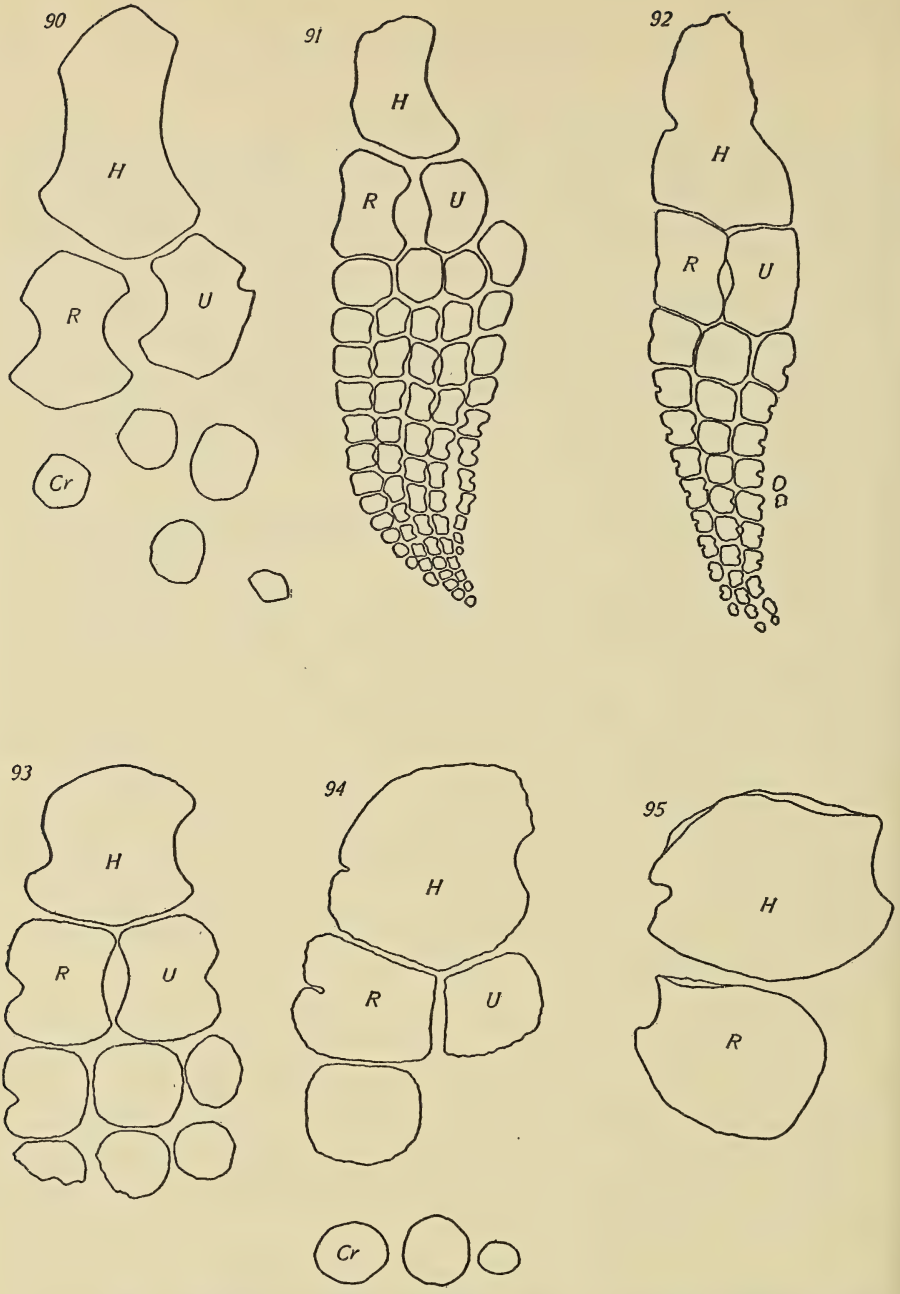
[25] The word "podial" is here intended to represent the metapodial and phalangeal regions.



FIGS. 90–95. Anterior limbs of Triassic ichthyosaurs. *H,* humerus; *R* radius; *U,* ulna; *Cr,* carpal.

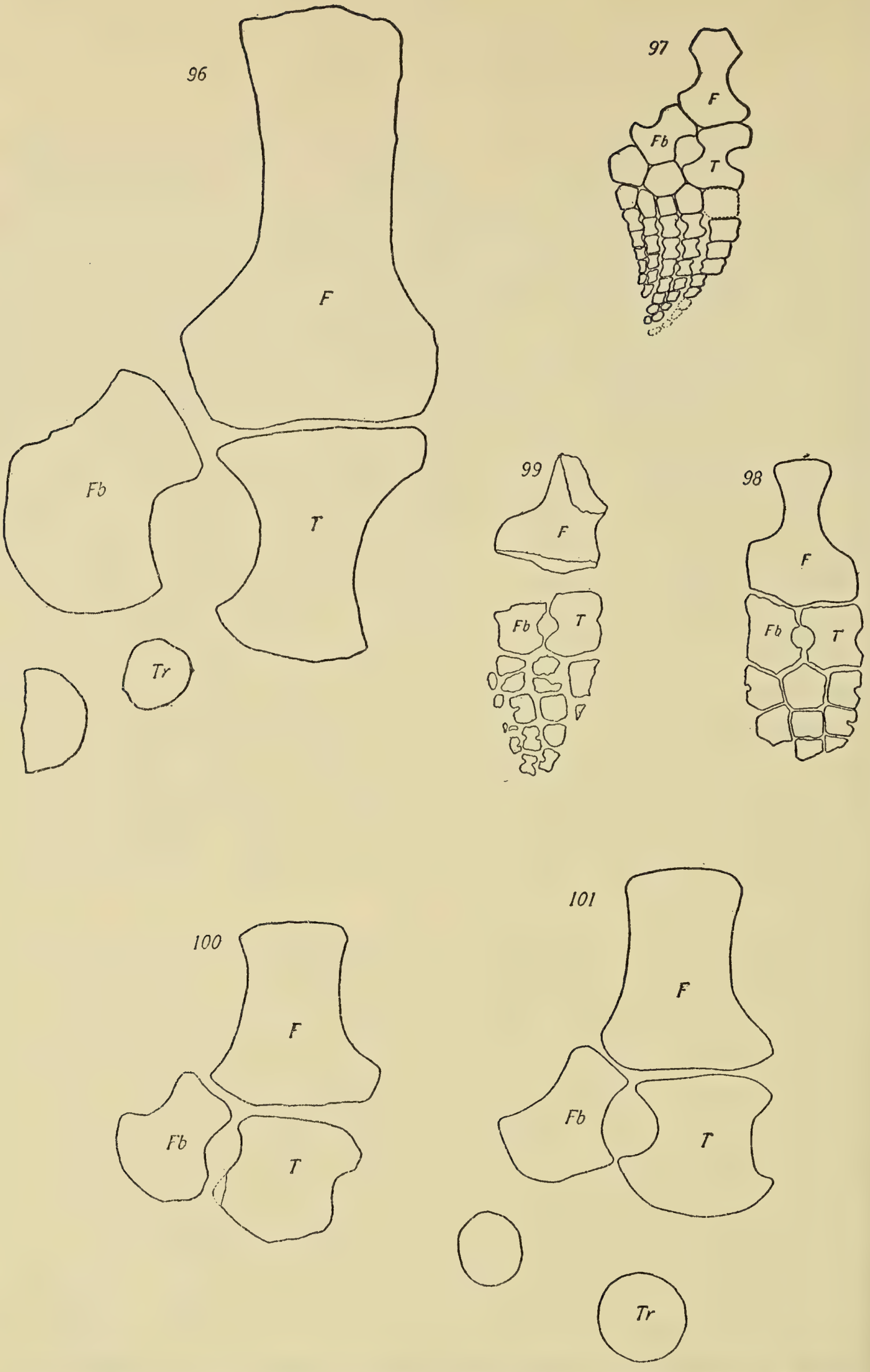
FIG. 90. *Cymbospondylus petrinus* Leidy, × $\frac{1}{10}$.
FIG. 91. *Mixosaurus cornalianus* (Bassani), × $\frac{9}{20}$. (After Repossi.)
FIG. 92. *Merriamia zitteli* (Merriam), × $\frac{9}{20}$.
FIG. 93. *Delphinosaurus perrini* Merriam, × $\frac{3}{10}$.
FIG. 94. *Shastasaurus osmonti* Merriam, × $\frac{3}{20}$.
FIG. 95. *Shastasaurus careyi* (?) Merriam, × $\frac{3}{20}$.

in the genus *Merriamia* with a narrow paddle, a relatively short podial region, three proximal mesopodials, a linear arrangement of the first and second rows of mesopodials, and but three functional digits. In both genera the characters mentioned appear in both anterior and posterior limbs. Of the four other genera recognized in the American Trias, *Delphinosaurus*, *Shastasaurus*, and *Toretocnemus* appear to have a type of limb-structure developed from some form like that seen in *Merriamia*. In *Toretocnemus*, in spite of the fact that the rib articulation is different from the other three genera, the limb structure is much like that of *Merriamia*. The American Middle Triassic *Cymbospondylus* may have a reduced phalangeal formula as in the Upper Triassic genera, and might be presumed to be related to these genera. It shows also a number of characters much like those of *Mixosaurus*, and may be nearer to that genus than are the American genera from the Upper Trias.

Mixosaurus and Cymbospondylus.—Probably the oldest limb elements known in the Trias consist of some isolated mesopodial or podial elements and a humerus from the Muschelkalk of Germany. The humerus which was described by Fraas (1891, pl. 3, fig. 5) is not materially different from that of *Ichthyosaurus*. These specimens occur in the same beds with material referred to *M* (*?*) *atavus* and probably belong in one of the forms included in that group.

Next to the lower Muschelkalk specimens of Europe, the earliest limb material is evidently that of *Cymbospondylus* (fig. 90) from the American Trias, closely followed in age by *Mixosaurus* (fig. 91) of the Italian Besano shales. The limb of *Mixosaurus* is fortunately preserved complete, showing all of the elements in position. In the known specimens of *Cymbospondylus* the podial region has not thus far been found undisturbed. These two forms represent the most primitive limb structure known in the Ichthyosauria. As the broad type of limb is possibly represented in one and the narrow type in the other, a comparison of the two is necessary in order to determine the common, or primitive characters.

The anterior and posterior limbs of *Cymbospondylus* were evidently not greatly different in size, the femur being apparently about one-sixth shorter than the humerus. In *Mixosaurus* the hind limb is relatively much smaller. The humerus and femur of *Cymbospondylus* are both relatively slender bones compared with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FIGS. 96–101. Posterior limbs of Triassic ichthyosaurs. *F*, femur; *T*, tibia; *Fb*, fibula; *Tr*, tarsal.

FIG. 96. *Cymbospondylus petrinus* Leidy, $\times \frac{1}{5}$.

FIG. 97. *Mixosaurus cornalianus* (Bassani), $\times \frac{3}{5}$. (After Repossi.)

FIG. 98. *Toretocnemus californicus* Merriam, $\times \frac{3}{5}$.

FIG. 99. *Merriamia zitteli* (Merriam), $\times \frac{9}{20}$.

FIG. 100. *Delphinosaurus perrini* Merriam, $\times \frac{9}{20}$.

FIG. 101. *Shastasaurus osmonti* Merriam, $\times \frac{9}{40}$.

the corresponding elements in other ichthyosaurians. In *Mixosaurus* the femur is slender, but the humerus may lack a median constriction, and have a transverse diameter almost equaling its length. In both genera the epipodial elements are relatively long compared with their own transverse diameter, or with the diameter of the proximal mesopodials. The radius is in both forms more slender than in other ichthyosaurian genera and is much narrowed in the median or shaft region. In *Mixosaurus* the ulna is convex posteriorly, having expanded somewhat on this side, as in the limbs of most aquatic forms. In *Cymbospondylus* the posterior border is expanded, but still shows a portion of the median or shaft region that has not been filled out by lateral expansion.

In the posterior limb of *Mixosaurus* the propodial and epipodial bones are more slender, and more strongly constricted in the median region, than are the corresponding elements of the anterior limb. In *Cymbospondylus* the femur is a little more slender than the humerus; the tibia is narrower distally than the radius, and the fibula has much the same form as the ulna.

In *Mixosaurus* the proximal row of the mesopodial region in the anterior limb consists of four elements of which the anterior three are the radiale, intermedium, and ulnare, in their normal positions. The fourth is a large pisiform set far up against the posterior margin of the ulna. In the typical *Cymbospondylus* three proximal elements are known but the form of the posterior side of the ulna suggests the presence of a pisiform as in *Mixosaurus*.

In *Mixosaurus* the podial region consists of five fingers, the number of phalanges in each of which is relatively small for an ichthyosaurian, not exceeding ten to eleven in the median digits. Many of the individual phalanges, particularly those in the proximal half of the phalangeal region and corresponding more nearly to the primitive phalangeal elements, are slightly elongated and show notches on one or both lateral margins, of such a form as to suggest an originally constricted shaft region.

In *Cymbospondylus* the podial elements have never been seen in complete series, but in several instances specimens representing parts of limbs show groups of three ossicles in rows, suggesting that possibly we are dealing here with transverse sections through mesopodial or podial regions with three digits. The borders of the rounded elements are not excavated or pitted as in *Shastasaurus*.

(See figs. 112 and 113.) In one specimen an element similar to the doubly notched phalanges of *Mixosaurus* is associated with limb bones.

Considering the common characters of the limbs of these two genera, the oldest of the ichthyosaurian forms, both are seen to have more primitive epipodials than appear in any of the later genera. There is also some suggestion that in *Cymbospondylus*, as in *Mixosaurus*, a largely developed pisiform element was present and in articulation with the posterior margin of the ulna. In so far as they are known to differ, *Cymbospondylus*, apparently the older genus, is more primitive, the humerus being more slender and longer in comparison with the longitudinal diameter of the mesopodials; while the ulna remains narrower through failure to close the posterior notch by increase of the transverse diameter. Excepting those more primitive features of *Cymbospondylus* mentioned above, the limbs of *Mixosaurus* appear to be the most primitive ichthyosaurian extremities known, and may serve as representatives of the fundamental forms from which the modified structures seen in the later Ichthyosauria have been derived. Particularly is this true of the podial portion of the limb which is so well shown in the Italian mixosaur specimens.

Though the suggestion has been made that the most primitive form of limb in the Jurassic Ichthyosauria possesses less than five digits,[26] it is probable that the pentadactyl form seen in *Mixosaurus* is at least as near the primitive type as the limb of any known genus. The suggestion that the most primitive ichthyosaurian limbs have less than five digits is based on the supposition that the short first digit has disappeared. As the ichthyosaurian limb was already in *Mixosaurus* a highly specialized paddle it is to be presumed that, if the first digit were to disappear at all, it would have been eliminated before the mixosaurian stage of evolution was reached. There are, therefore, the alternative hypotheses that the mixosaur paddle retains the primitive five digits and is the most primitive known, or that, after having lost digit number one, it has brought the number of phalangeal rows up to five again by developing a digit not represented in the original five, and is therefore not a particularly primitive type.

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[26] Lydekker, R., Geol. Mag., 1888, Dec. 3, vol. 5, p. 310.

In the development of the paddle in some aquatic animals there has been a tendency to eliminate the first digit, but this is by no means always the case. Judging from all the suspected relationships of the Ichthyosauria there is good reason to suppose that the ancestors of this group were forms possessing five digits. If such be the case, the general primitiveness of the mixosaurian limb, and the fact that this is the most ancient paddle of which the podial region is known, suggest that the digits seen here are the primitive five phalangeal series.

Another possibility, which should perhaps be borne in mind, is that the early ancestor possibly had only three or four digits. From what we know of the primitive reptilian groups this seems improbable, but the fact that all of the genera of the American Upper Triassic show a paddle structure of this nature, and that there is reason for suspecting the occurrence of a similar structure in the Middle Triassic *Cymbospondylus* lends some appearance of reasonableness to this hypothesis.

The form of the paddle and the arrangement of the mesopodial elements in *Mixosaurus* in some ways closely resemble the structure seen in the latipinnate forms of Ichthyosaurus (figs. 104 and 105). In both cases the paddle is relatively broad, and the third element of the second row of mesopodials articulates proximally upon the intermedium. In the longipinnate forms of *Ichthyosaurus* (fig. 102), as in the American Upper Triassic genera, the third element of the second row articulates with the posterior element of the first mesopodial row and not at all, or only incidentally, upon the intermedium. The structure seen in *Mixosaurus* appears more primitive than in the other forms, and seems also to show that no rearrangement of the digits has been made through addition to, or subtraction from, the original number.

As to the definite relationship of the forms with the mixosaurian type of paddle to the typical Latipinnati of the Jurassic, and to the more specialized forms of the *Baptanodon* type, there may be some doubt, as the largely developed pisiform of *Mixosaurus* is not necessarily present in the Latipinnati. According to Baur's view (1887, 1) the pisiform of *Mixosaurus* has ultimately become the third or posterior epipodial element in *Baptanodon* (fig. 107). There may, however, be some question as to such a transition through *Ichthyosaurus*. Though a small proximal element of the posterior podial row may overlap the most posterior of the three elements of the first mesopodial row, it is difficult to demonstrate that the large pisiform of *Mixosaurus* has been continued through *Ichthyosaurus* to *Baptanodon*. As has been shown by Fraas (1891, pp. 27 and 30), the intermedium may come into articulation with the propodial element and thus furnish opportunity for development of the *Baptanodon* type of limb in any one of several groups.

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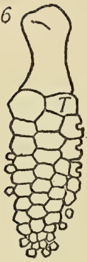

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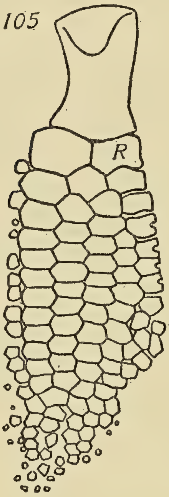

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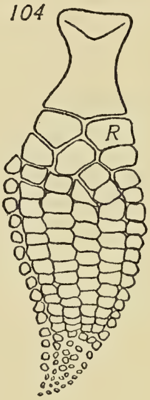

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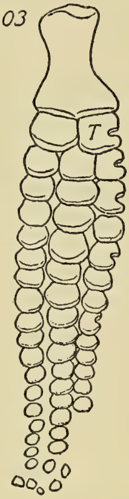

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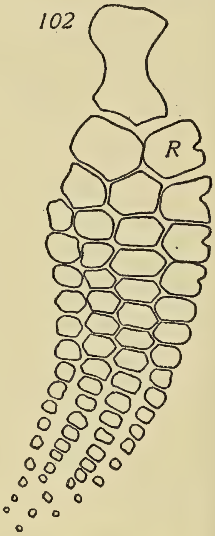

FIG. 102. *Ichthyosaurus quadriscissus* Quenstedt. Anterior limb, about $\frac{1}{3}$ natural size. *R*, radius. (After Fraas.)

FIG. 103. *Ichthyosaurus acutirostris* Owen. Posterior limb, about $\frac{1}{6}$ natural size. *T*, tibia. (After Fraas.)

FIG. 104. *Ichthyosaurus communis* Conybeare. Anterior limb, about $\frac{1}{3}$ natural size. *R*, radius. (After Lydekker.)

FIG. 105. *Ichthyosaurus intermedius* Conybeare. Anterior limb, about $\frac{2}{9}$ natural size. *R*, radius. (After Lydekker.)

FIG. 106. *Ichthyosaurus intermedius* Conybeare. Posterior limb, about $\frac{2}{9}$ natural size. *T*, tibia. (After Lydekker.)

Boulenger (1904) has also shown that in *Ichthyosaurus extremus* (fig. 108), even though it be of the latipinnate type, the third element in articulation with the propodial is the intermedium. It is also interesting to note that Broili[27] has recently described a broad-paddled form (fig. 109) which he refers to the Longipinnati.

Some suggestions as to the possibility of rearrangement of the

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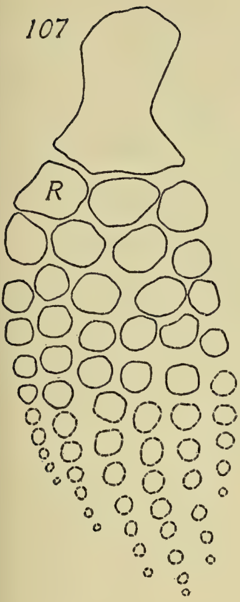
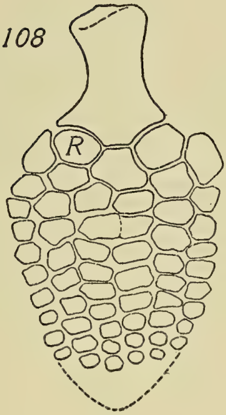
[27] Broili, F., Palaeontog., Bd. 54, p. 151.





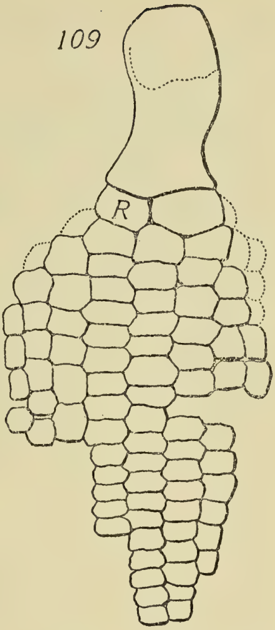
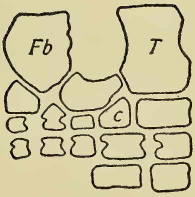


Fig. 107. *Baptanodon discus* Marsh. Anterior limb, about $\frac{1}{8}$ natural size. *R*, radius. (After Marsh.)

Fig. 108. *Ichthyosaurus extremus* Boulenger. Anterior limb. *R*, radius. (After Boulenger.)

Fig. 109. *Ichthyosaurus platydactylus* Broili. Anterior limb, much reduced. *R*, radius. (After Broili.)



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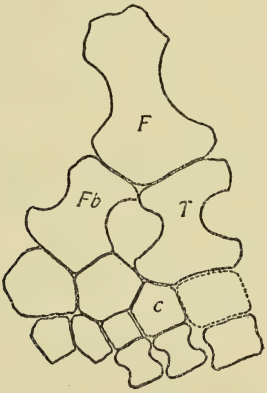

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Fig. 110. *Mixosaurus cornalianus* (Bassani). Posterior limb, about natural size, from rough sketch by the author. *T*, tibia; *Fb*, fibula; *C*, a distal carpal?

Fig. 111. *Mixosaurus cornalianus* (Bassani). Posterior limb, natural size. (After Repossi.) *F*, femur; *T*, tibia; *Fb*, fibula; *C*, a distal carpal?

elements of the mesopodial region are perhaps to be found also in the structure of the posterior limb of *Mixosaurus*. In the first row of the mesopodial section of the hind limb figured by Repossi (fig. 111), as in the anterior limb, four elements appear instead of three. The structure which appears in this case is unusual, but is probably explained by another specimen in the Milan museum (fig. 110) in which only three elements are present in the proximal row. The lunate intermediate element almost closes the gap between the tibiale and fibulare, but in a second row of bones three elements articulate with the distal border of the intermedium; of these the anterior one has crowded up between the tibiale and intermedium so as almost to come in contact with the tibia. In the specimen figured by Repossi, this element of the second row seems to have reached the tibia. This explanation not only accounts for the fourth element of the proximal row, but may also explain the presence next the posterior border of tarsale one, and apparently functioning as tarsale two, of an element showing a strong median constriction. This bone has the appearance of a metapodial or phalange, and if the explanation given above is correct, is really a metapodial moved upward into the position of tarsale two.

Judging from the other relationships indicated in the characters of *Mixosaurus* there seems to be reason for considering that the genus is possibly not ancestral to any form of *Ichthyosaurus*, but is associated more closely with those forms in which the inferior rib head has been almost entirely lost. If such be the case, the broad type of paddle in *Mixosaurus* is evidently an independent expression of a tendency similar to that shown in the broad-paddled forms of *Ichthyosaurus*.

Merriamia.—The only Upper Triassic form in which the structure of the entire limb is known is the genus *Merriamia*, from the upper portion of the Upper Trias of California. In this type the manus (fig. 92) is relatively slender and includes only three functional digits with the faint rudiment of a fourth behind these. The humerus is relatively slender and shows a median constriction. The radius and ulna are one-half as long as the humerus and are separated by a large opening. Beyond the first row of the carpus, the limb elements are arranged in three well defined linear series, between which there is no interlocking. The metapodial and phalangeal elements are all more slender than in *Ichthyosaurus*.

The elements of the two outer rows are all notched on the outer border, and in many instances a median constriction is developed. In the middle digit lateral notches are present only on the posterior border of the elements beyond the first phalange. Including the minute discoidal terminal elements, there are eight phalanges in the middle digit and seven in the first and third. In this genus the hind limb (fig. 99) is relatively small.

In contrast with the form of paddle seen in *Mixosaurus* that of *Merriamia* is exceedingly narrow, and the podial portion is also relatively short. The function of the paddle was evidently somewhat different from that in *Mixosaurus*. The relatively longer humerus and shorter podial region apparently gave the limb somewhat more freedom of movement than in the case of the limbs with shorter humerus and larger podial region as in *Mixosaurus* and other broad-paddled ichthyosaurians.

Toretocnemus.—The anterior limb of *Toretocnemus* is unfortunately known only in part (fig. 139), but in as much of it as is present the structure resembles that in *Merriamia*. Only digits one and two are preserved and in these the terminal phalanges may be missing, but the fourth element of digit one and the third of digit two are so small that the total number could hardly have been larger than in *Merriamia*. The posterior paddle in this genus (fig. 98) is also much like that in *Merriamia*, and the presence of a rudimentary fourth or posterior digit is indicated by small facets on the posterior margins of the elements of the third digit. In *Toretocnemus* the posterior limb is as large as the anterior one.

Delphinosaurus and Shastasaurus.—In both *Delphinosaurus* and *Shastasaurus* the propodial and epipodial limb elements are shortened as compared with the limb of *Merriamia*. In *Delphinosaurus* (fig. 93) the humerus is scarcely longer than broad, but retains a distinctly contracted shaft region. In *Shastasaurus* (figs. 94 and 95) the humerus may be so greatly abbreviated that its width considerably exceeds its length.

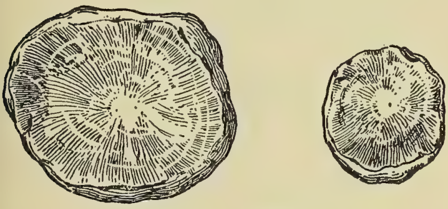
In *Delphinosaurus* the radius and ulna are of nearly equal size and the ulna differs from that of all other ichthyosaurs excepting *Cymbospondylus* in showing a posterior notch and a median constriction similar to that of the radius. In *Shastasaurus* the greatly shortened radius has a narrow notch on the anterior border while the posterior side is either only very slightly concave or is distinctly convex as in *S. careyi*. In that species is found the only exception to the rule that in the Triassic Ichthyosauria the radius and ulna are separated by a distinct cleft. In *Shastasaurus osmonti* the posterior border of the ulna is convex.

Although the phalangeal region of the limbs of *Delphinosaurus* and *Shastasaurus* has not been seen in its natural arrangement in connection with the remainder of the limb, there seems to be a strong reason for believing that it was of a reduced and presumably tridactyl type as in *Merriamia* and *Toretocnemus*. In *Delphinosaurus* where the radius and ulna are of nearly equal size, there are three elements each in the first and second rows of the mesopodial region as in *Merriamia*, but the posterior elements in both rows are much smaller than the others and much smaller than in *Merriamia*, suggesting that the posterior digit was relatively small. In *Shastasaurus* the radius is much larger than the ulna. The radiale, the only mesopodial which has been found in place, is considerably larger than in any of the other genera, and even exceeds the ulna in size. Evidently in this form the space for the posterior digits was considerably narrower than in *Delphinosaurus*, which suggests that *Shastasaurus* may have had only two well developed digits and a rudimentary third.

Though no series of paddle bones showing the form and arrangement of the elements in the podial region of *Shastasaurus* has as yet been discovered, in several cases a number of scattered bones representing mesopodials or phalanges have been found with other parts of the skeleton, but it has not been possible in any instance to make certain of their position in the paddle. With specimen 9081 a number of discoidal bones are associated with the elements of the shoulder girdle and the proximal portion of the limb. Three of these not far from the radius appear from their position to represent a transverse row from the proximal portion of the paddle (*Cr.* fig. 94). At one end of the row the ossicle is much smaller than either the median one or the one at the opposite end. While it is not possible to make sure whether the elements seen here belong in the podial or in the mesopodial region, the evident reduction of one of the terminal bones supports the evidence for reduction of the third or posterior digit as suggested above.

In several of the specimens of *Shastasaurus* discoidal ossicles present with the limb elements are deeply pitted or grooved around the margins (fig. 113; also pl. 15, figs. 3 and 4). This structure, with the circular outline developed, evidently indicates that they were embedded in heavy cartilage plates as in *Baptanodon* (fig. 114). The only instance in which other than discoidal elements have seemed to represent the distal portion of the paddle in *Shastasaurus* is in the type specimen of *S. altispinus* (pl. 18, fig. 4), in which there are two ellipsoidal bones sharply notched at one end, but with the margins grooved and pitted. The notches evidently indicate that the bones were on the margins of the paddle.

In both *Delphinosaurus* and *Shastasaurus* the femur is more slender than the corresponding elements of the anterior limbs. (See figs. 100 and 101.) The tibia is relatively large compared with the small fibula. Both tibia and fibula show a median constriction. Of the elements beyond the epipodials only a few discoidal ossicles are known.



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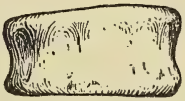

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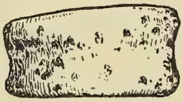

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FIG. 112. *Cymbospondylus petrinus* Leidy. Metapodials or phalanges, × ½.
FIG. 113. *Shastasaurus osmonti* Merriam. Metapodial or phalange, marginal view, × ¾.
FIG. 114. *Baptanodon* sp. Phalange, marginal view, × ¾.

STAGE OF EVOLUTION OF TRIASSIC ICHTHYOSAURS

In viewing the Ichthyosauria collectively there seems to be no reason for questioning the unity of the group. Throughout the entire series of forms in which the history of the order is represented there is no doubt as to relationship; the oldest and the youngest members showing so strong a resemblance to the typical genus that no question as to their common descent has arisen. In comparing the oldest forms with the latest there is, however, a strong contrast in the structure of many of the important parts of the skeleton, and the differences are of such a nature and so graded in time as to suggest progressive specialization of a very definite type.

A list of characteristics in which the Triassic and the later Jurassic ichthyosaurs are found to differ would include the following:

LATER JURASSIC FORMS	TRIASSIC FORMS
1. Locomotion almost solely by means of powerful vertical caudal fin.	1. Locomotion assisted to a greater extent by paddles than in the Jurassic forms.
2. Limbs much abbreviated, and functioning largely as fins rather than as paddles. Epipodials reduced to the form of mesopodials.	2. Limbs relatively large and with important function as paddles. First two segments relatively long.
3. Hind limbs relatively small.	3. Hind limbs relatively large.
4. Epipodial, metapodial, and phalangeal elements reduced to polygonal plates, or to approximately circular discs with concave margins.	4. Epipodial, metapodial, and phalangeal elements often elongated, and with shafted median region.
5. Number of phalanges in each digit greatly increased.	5. Number of phalanges in each digit relatively small.
6. Number of digits often greater than five.	6. Number of digits not increased beyond five.
7. Pelvis much reduced: in later forms with ischium and pubis fused.	7. Pelvic elements heavy: inferior elements much expanded. Ischium and pubis never fused.
8. Pelvis loosely connected with body.	8. Upper end of ilium broad, indicating somewhat firmer connection with vertebral column than in *Ichthyosaurus*.
9. Skull much elongated, and relatively large compared with the trunk.	9. Skull shorter compared with length of the trunk.
10. Jaws slender and much elongated.	10. Jaws generally relatively short.
11. Maxillaries relatively small; premaxillaries relatively large.	11. Maxillaries relatively long, and premaxillaries relatively short.
12. Orbits greatly enlarged. Superior temporal opening small, bar behind orbit very narrow.	12. Orbits relatively small, temporal bar behind orbit broad.
13. Auditory apparatus consisting of massive elements adapted to use in deep diving.	13. Element supposed to represent stapes relatively small.
14. Teeth numerous, simple-conical, loosely attached.	14. Teeth numerous in *Cymbospondylus*, relatively few in *Mixosaurus*. Teeth set in pits in older forms.
15. Vertebral centra high, relatively short anteroposteriorly.	15. Vertebral centra averaging relatively long and low.
16. Neck short, usually with two or more anterior cervical centra fused.	16. Neck region short, but anterior cervical centra all separated by wide intervertebral spaces.
17. All discrete cervical and caudal intercentra apparently lost in some late forms, elements of lower arches not united ventrally.	17. Cervical intercentra few and small. Caudal intercentra large and united ventrally to form Y-shaped lower arches.

Later Jurassic Forms (*continued*)	Triassic Forms (*continued*)
18. Zygapophysial facets of vertebrae reduced or brought into one plane and united.	18. Zygapophysial faces in the anterior half of the vertebral column neither united nor brought into the same plane.
19. Neural spines of vertebrae strongly flattened laterally.	19. Neural spines averaging relatively thick, and may be circular in cross-section in the anterior half of the vertebral column.
20. Posterior region of tail bent downward sharply for support of lower lobe of fluke.	20. Distal region of tail showing relatively less marked downward curvature. Sometimes bent upward strongly, and then downward.
21. Neural arches of caudal region reduced near bend of tail, owing to change of form of fluke.	21. Neural arches in middle third of caudal region not reduced. In some cases the arches in this region are much elongated and erected to broaden this region of the tail.
22. Scapula narrowed distally.	22. Scapula expanded distally.
23. Episternum T-shaped instead of deltoid.	23. Episternum approaching a deltoid rather than T-shaped form where known (*Mixosaurus*).
24. Abdominal ribs often not united along median line.	24. Abdominal ribs heavy, and united in a prominent spine on the median line.

It will be noted that in the extended series of differences which appear in the table above, nearly all are features of the skeleton which have been considered as standing in close relationship to aquatic adaptation. These include also the principal ordinal characteristics distinguishing the group. The last three characters only are not considered as necessarily standing in close relation to aquatic adaptation, but possibly even these are to be ascribed to the effect of adaptation of this nature. In the contrast between the earlier and the later ichthyosaurians it is seen that nearly all of the characters of the later forms which are considered as standing in close relationship to aquatic adaptation are less distinctly expressed in the Triassic representatives of the group. In other words the characteristics of the earlier forms are practically all nearer those of shore or land reptiles, and those of the later ones take the direction of specialization toward an adapted fish-like form. The evidence before us shows that the trend of the specialization of the Ichthyosauria has been to develop those features which are of importance in purely aquatic life, and to reduce in importance those structures which have little or no function in such an environment as would be met under aquatic conditions.

In the earlier stages of the study of the Ichthyosauria various opinions were expressed[28] as to whether the characters showing close relation of these forms to their aquatic environment were survivals from a very primitive fish-like ancestral type, or whether they were secondarily acquired through accommodation of a land type to life in the sea. Practically all investigators who have expressed themselves on this point in recent years have held to the opinion first given a basis of observed fact by Baur (1887, 2), *viz.*, that the ichthyosaurs are specialized aquatic forms occupying in the Reptilia a position similar to that of the cetaceans in the Mammalia. This view receives support amounting to a demonstration from the evidence gathered in a study of the history of the group. Not only is the stage of evolution of the Triassic representatives nearer the shore or semi-aquatic reptilian type than in the later ones, but a definite and fairly regular gradation or progressive specialization from the earliest forms to the latest seems to be recognizable in many parts of the skeleton. The evidence of gradual modification toward the fish-like type presents itself not only in a comparison of the types of the successive periods with each other, but it is almost as distinctly seen in contrasting the forms of the latest Triassic with those from the middle division or from the lower part of the Upper Trias. It is clearly noticeable again in contrasting the faunas of the Upper and Lower Lias, or in a comparison of the Upper Liassic species with those of the later Jurassic and Cretaceous. Taken as a whole the evidence is of such a nature as to leave no room for doubt as to the course of evolution of the known representatives of the Ichthyosauria. While we are unfortunately not able to see back to the beginning of the evolutionary history, extending from the Middle Trias to Cretaceous, it can hardly lead from any other than a typical reptile with extremities constructed largely, if not entirely, for ambulation.

In the evolutionary series beginning with the unknown crawling ancestor of the ichthyosaur, Middle Triassic forms of the type of *Cymbospondylus* represent a stage in which the animals had already abandoned the shore as a place of regular habitation, but still retained in their skeletal structure enough original characteristics to give a clue to their origin. Contrasted with the Middle Triassic *Cymbospondylus* type we have at the latter end of the series such forms as the *Baptanodon-Ophthalmosaurus* group in which the adaptation to life in deep water is so extreme as to have suggested to otherwise careful investigators that these forms were less specialized than any other reptiles.

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[28] Gegenbaur, C., Untersuchungen zur vergleichenden Anatomie der Wirbelthiere, 2 Heft., 1865. Paddles derived from selachian fins.

Haeckel, E., Generelle Morphologie der Organismen, Bd. 2, p. 134, 1866. Resemblance to fish secondarily acquired.

Origin of Ichthyosauria

Though the ichthyosaurs were throughout their whole known history constantly specializing along the line of adaptation to their aquatic environment, we find that as early as the Middle Triassic they were already in the class of the highly specialized aquatic reptilian types. From what we know, we can hardly suppose them to have separated themselves from the parent shore type far enough to be called ichthyosaurs later than the early part of the Trias. Possibly their origin dates from an even earlier period. There seems, therefore to be good reason for considering them one of the oldest of the reptilian orders. The primitive ichthyosaur was evidently a typical reptile, and considering the necessarily early period of its origin, antedating as it does that of most of the other orders, it may be derived only from one of the very primitive members of this class. Unless we consider the ichthyosaurs as themselves one of the primitive divisions of the Reptilia, we have only the most primitive representatives of the cotylosaurian, synapsidan and diapsidan stems with which it may stand in the relation of descent.

Woodward[29] has included the ichthyosaurs in the reptilian group in which the skull possesses a single temporal arcade, along with the Anomondontia, Sauropterygia and Chelonia; at the same time calling attention to the very primitive characters of the skull. Cope,[30] in one of his last phylogenic arrangements of the reptilian orders, derived the Ichthyosauria directly from the primitive Cotylosauria.

Broom[31] has separated the ichthyosaurs from both the Synapsidan and Diapsidan groups. More recently Williston[32] has called attention to the fact that "the presence of an original lateral temporal opening is by no means proved." Baur[33] considered the ichthyosaurs rhynchocephalian. McGregor[34] and Osborn [35] have suggested close relationship of the Ichthyosauria with the Rhynchocephalia.

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[29] Woodward, A. Smith, Vertebrate Palaeontology, p. 143, 1898.

[30] Cope, E. D., Primary Factors of Organic Evolution, p. 115, 1896.

[31] Broom, R., Proc. Zool. Soc. Lond., 1901.

[32] Williston, S. W., Biological Bulletin, vol. 7, p. 186, Sept. 1904.

Excepting in those characters indicating adaptation to aquatic environment the ichthyosaurian skeleton is undoubtedly very primitive. Whether it has been diaptosaurian, synapsidan or cotylosaurian in its original form is less certain.

Some of the most definite opinions regarding relationship to other groups are those of the several writers who have considered the Rhynchocephalia the ancestral type. While the Ichthyosauria show a strong resemblance to these diaptosaurians in many characters, it is to be questioned whether this similarity is more than a survival of common primitive characters in both. At any rate, if it be shown that a number of the most characteristic features of the Diaptosauria are lacking in the Ichthyosauria we shall hardly be justified in considering the diaptosaurs as their ancestors.

Recently McGregor[36] has expressed the opinion that the diapsidan order Phytosauria includes the nearest known relatives of the ichthyosaurs, and that they represent the nearest approximation to the amphibious form through which the ichthyosaurs passed in their evolution from rhynchocephalian-like ancestors, "though no *known* phytosaurian can actually be the ancestor of the Ichthyopterygia."

The phytosaurs and the ichthyosaurs have many characters in common, and particularly the phytosaurs show some affinity with the most primitive diaptosaurians. There are, however, a number of characters which seem to indicate that the phytosaurs and ichthyosaurs have arisen quite independent of each other. In order also to have the appearance of being intermediate between the ichthyosaurs and the primitive diaptosaurs, the phytosaurs should precede the ichthyosaurs in time. We find, however, that the phytosaurs belong mainly to the latter part of the Upper Triassic, while the ichthyosaurs were a sharply differentiated and highly specialized group early in Middle Triassic time, and had already expressed in them most of the characters which separate their Jurassic representatives from the phytosaurs. In spite of the fact that the orbits were much smaller in the earlier ichthyosaurs than in the later genera, and that the inferior temporal arcade was large enough so that a primitive lateral opening would not necessarily be closed by contraction of the bar, this lateral opening is not present as in the Phytosauria. There are also no antorbital and no external mandibular vacuities in the ichthyosaurs; the squamosal and supratemporal are not fused; the pleurocentrum of the atlas was large; no ectopterygoid is certainly known; a large pineal foramen was present; the exoccipital and opisthotic were not fused; there was no tendency to develop a secondary palate; the pterygoids were in contact with the basioccipital; and the thoracolumbar vertebrae were more numerous than in the phytosaurs.

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[33] Baur, G., Am. Nat., vol. 21, p. 837, 1887.

[34] McGregor, J. H., Science N. S., vol. 16, p. 27, July 4, 1902. Also, Mem. Amer. Nat. Hist., vol. 9, part 2, p. 91, Feb. 1906.

[35] Osborn, H. F., Mem. Amer. Mus. Nat. Hist., vol. 1, No. 8, p. 456, Nov. 1903.

[36] McGregor, J. H., Op. cit., p. 89.

The phytosaurs are typically rhynchocephalian in more characters than the ichthyosaurs. The main features in which they show special similarity to the ichthyosaurs are found in the structure of the rostrum and the nasal region. The median position of the nares appears, however, almost a normal character of marine air-breathing vertebrates, and the extension of the premaxillary region occurs in the development of an elongated snout in most groups of reptiles excepting the Crocodilia and Choristodera; so that in the case of the Phytosauria the peculiar feature is the presence of an elongated snout with median nares in a fresh-water form not otherwise highly specialized. The significance of this parallelism is possibly no more than that the phytosaurs are not necessarily crocodilian, rather than that the ichthyosaurs are modified phytosaurs.

It seems that the characters in which the phytosaurs and ichthyosaurs differ at least balance the special resemblances which may be common inheritances from very early ancestors. It also appears easily possible that the time of origin of the ichthyosaurs was at so early a date that some diaptosaurian characters, as the lateral temporal opening, have never appeared in them. The phytosaurs are not far removed from the typical Diaptosauria. They may have originated early or may have had their origin in the latter part of Middle Triassic time. It is doubtful whether their peculiarities, aside from very primitive features which parallel characters in the ichthyosaurs, existed in the phytosaurs as early as the time of origin of the Ichthyosauria. It is not improbable that the phytosaurs simply parallel to some extent the amphibious type through which the ichthyosaurs must have passed in their evolution, and that they developed as a distinct phytosaurian group after the ichthyosaurs had become typical marine animals.

Variation in the Ichthyosauria

The Ichthyosauria exhibit through the whole range of the order such a constancy in the major features of their skeletal plan that no question has ever arisen as to whether a particular form is properly considered as a member of the group. There is, however, a considerable range of variation in certain important groups of characters, and indefiniteness rather than fixity of generic and specific features seems to be the rule in the better known forms. Though the variability is shown to some extent in all parts of the skeleton it appears in its most extreme form in those structures which are most distinctly modified in adaptation to aquatic life.

An example is seen in the paddles of *Ichthyosaurus*, the fundamental structure of which has always remained much the same. In the podial region the digits have always held close together, in contrast to the divergent fingers of the mosasaurian type; and the phalanges have increased greatly in number, with accompanying average shortening. The number of digits has however varied between *Ichthyosaurus communis* with a possible ten longitudinal rows of phalanges, and *I. acutirostris* with three, or *Shastasaurus* probably with two and a rudimentary third. With the variation in the number of digits, the number of the phalanges and the form of the paddle have generally varied, so that the many fingered paddle of *I. communis* is broad but short, and the paddles of *I. acutirostris* are excessively long and slender. The two types of paddles represented by *I. communis* on the one hand, and *I. platyodon* with *I. acutirostris* on the other hand, distinguish two groups of ichthyosaurs which are in the main fairly distinct (figs. 103 and 104). They were separated by Kiprijanoff[37] as Latipinnipedes typified by *I. communis*, and Longipinnipedes represented by *I. platyodon*; but were not designated as genera, as there seemed to be no point at which a dividing line could be drawn satisfactorily.

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[37] Kiprijanoff, M., Mém. l'Acad. Imp. d. Sc. St. Petersburg, VII ser., t. 28, no. 8, p. 88.

This classification was accepted, in somewhat modified form, by Lydekker[38] in preparing his catalogue of fossil reptiles of the British Museum, the group names being changed to Latipinnati and Longipinnati. The groups have been recognized by Fraas and other investigators who have made particularly close studies of the structure and relationships of the Ichthyosauria. Fraas accepted the divisions Longipinnati and Latipinnati but treated them as groups, and not genera, as had been done by Kiprijanoff and Lydekker. More recently they have been designated as distinct genera by Jaekel[39] and Boulenger.[40]

If the longipinnate and latipinnate divisions of the ichthyosaurs of the Lower Lias actually represent distinct groups of species tending to specialize in somewhat different directions, they should be recognized as separate genera. It is, however, true that most of the investigators who have worked over large collections have found the separation of the two divisions so difficult that they have refrained from giving generic values to them.

To a considerable extent the same difficulties that are met in this grouping of Jurassic species of the true ichthyosaurs are found in the definition of other genera and species. The species of *Ophthalmosaurus* and *Baptanodon* appear quite widely separated from the typical forms, but in reality most of the characters which separate them from *Ichthyosaurus* are to be found in various forms of *Ichthyosaurus* itself.

The statements which have been made regarding variation in the structure of the paddles might apply almost as well to most other portions of the skeleton in which characters of generic or specific rank appear, as in the facial region of the skull, the dentition, and the caudal fin. A general study of the considerable variations occurring inside the Ichthyosauria seems to show fewer interruptions between the various forms recognized than commonly appear in natural groups. These facts apparently indicate a high degree of plasticity in the ichthyosaurian types of Jurassic time. Judging from the number of forms known in the Trias this plasticity was at least as pronounced in that period.

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[38] Lydekker, R., Geol. Mag. London, 1888, Dec. 3, vol. 5, p. 310. Also Catlg. Foss. Rept. and Amphib. Brit. Mus., pt. 2, p. 13, 1889.

[39] Jaekel, O., März-Protokoll d. Deutsch, geol. Gesel., Bd. 56, Jahrgang 1904, p. 32. Jaekel proposed the name *Eurypterygius* for the latipinnates, and *Stenopterygius* for the longipinnates.

[40] Boulenger, G. A., Proc. Zool. Soc. Lond., vol. 1, p. 425, Aug. 2, 1904. Boulenger uses the generic name *Ichthyosaurus, sensu stricto*, for the Latipinnati; and *Proteosaurus* Home for the Longipinnati.

The plasticity, or the greatest variation, in ichthyosaurs has appeared in those portions of the skeletal structure which stood in the most immediate relation to their environment, and could be most easily modified by changes in habits, food, or any variation in the elements of their surroundings. The most variable portions of the skeleton are probably the paddles and the caudal fin. In many of the principal characters of the cranial region of the skull a most remarkable conservatism is shown; only in the form of the rostrum and in the nature of the orbit do we find variation comparable to that of the limbs. The significance of the location of the centers of greatest variation seems to be that the variation is to a great extent determined by the peculiar relation of the animal to its environment, and in those centers where no distinctly important relation of this nature exists variation has been insignificant.

The fact that the different ichthyosaurian forms recognized are not easily separable offers some support to the view that they represent stages in a differentiation of the group which has taken place at a fairly uniform rate, and has not therefore given us sharply distinguished and persistent resting stages, such as have sometimes been considered to represent genera and species.

In so far as the above suggestions hold good, the evolution of these forms may indicate that the species have originated either as the direct result of use and disuse due to pressure of the environment; or that they have arisen as variants or mutants in which the direction of mutation has been determined by the same external factors which would be supposed to direct use and disuse in the application of the Lamarckian hypothesis. According to this suggestion the known ichthyosaurian types may be explained as having arisen under slightly different sets of conditions, either at the same time in different places, or at different times in the same place.

Whatever be the ultimate cause of the progressive specialization seen in the Ichthyosauria, this tendency became almost a constitutional feature. In spite of minor variations and of the inclination of geographically separated types to take somewhat different paths in their specialization, the general trend of evolution of all forms over the earth has been in the same direction, and at about the same rate. In most instances the horizon in which a Triassic ichthyosaur belongs may be determined by the degree of specialization of any one of a considerable number of structures, as *e. g.*, the zygapophyses of the vertebrae. Where characters of late forms seem to appear in early ones, the average of the characters of the whole organism will be found to indicate a relatively low level of specialization. In the tail of the Middle Triassic *Cymbospondylus* the reduced upper arches of the distal caudal region suggest a caudal series like that of the later *Ichthyosaurus*, but the vertebral centra of this region in *Cymbospondylus* offset the beginning specialization of the arches by preserving a remarkably high and compressed or primitive form.

The tendency which the Ichthyosauria have shown to keep the same general trend of specialization through their whole history, and in all geographic regions, is not contrary to the suggestion advanced above; *viz.*, that the modifications introduced in this group usually indicate the bringing about of a closer relation to their environment. The all important feature which distinguishes the Ichthyosauria as an order is their aquatic adaptation. Entering as they have into a realm very different from that in which the immediately ancestral types have lived, the factor which has overshadowed all others has been the necessity of getting a working basis for life in water, particularly with relation to locomotion. The extent of the changes required in the accommodation of all ichthyosaurians, whenever and wherever they have existed, to those simpler features of aquatic life which are the same in all periods and in all places may be responsible in a large measure for the generally similar trend of evolution.

In this connection we naturally enquire why it was necessary for the Ichthyosauria to leave their original environment, for surroundings in which an entirely different equipment was necessary. The only explanation which offers itself suggests a possible change of food habits, through the discovery that certain of the thriving cephalopod groups of the early Mesozoic furnished an abundant and easily obtained food supply. Even in the most favorable light, however, the problem of definite variation in the Ichthyosauria in some of its aspects seems to invite a resort to orthogenesis; or to the view that there are factors influencing variation which are not as yet understood, and that these tendencies to similar variation may express themselves in related groups for long periods, and in regions widely separated geographically.

Taking the history of the Ichthyosauria from the earliest stages to the latest, the following statements regarding the group seem to be warranted by the known succession of forms: (1) The group is unquestionably a unit, and no doubt has arisen as to the common origin of the forms included in it. (2) There has been a very considerable advance in specialization extending through a long period. (3) Variation has been greatest in those structures standing in the closest relation to aquatic adaptation. (4) Variation seems generally to be of the continuous rather than of the saltatory type. (5) Variation is remarkably direct, or takes much the same course in all forms of the same geological age.

Classification of the Ichthyosauria

After some knowledge had been obtained of types distinct from *Ichthyosaurus*, the earliest attempt at classification of the groups included in the Ichthyosauria was that of Baur (1887, 2), in which three families, the Ichthyosauridae, Baptanodontidae, and Mixosauridae, were established. To these Merriam has more recently added a fourth group, the Shastasauridae (1902, 2). At the time when these families were described the arrangement of the ichthyosaurian forms seemed fairly simple, but in reality comparatively little was known regarding any of these groups excepting the Ichthyosauridae. Since that time the principal points in the structure of *Mixosaurus* have been made known by Repossi (1902), the material available for study of the American Triassic forms has very greatly increased, and large additions have been made to our knowledge of the structure of *Baptanodon*[41] and *Ophthalmosaurus*.[42]

With the recent increase in the available information, many points of relationship have been determined among the ichthyosaurian forms, but the tendency on the whole has been to make a satisfactory arrangement more difficult than before. While the four families already described may still be recognized as fairly distinct groups, they do not adapt themselves to a phylogenic scheme such as would seem to be demanded by the long historic series now known, and in which cognizance is taken of the facts of geographic distribution. The evolutionary history of the Ichthyosauria now extends from the Middle Triassic to the Cretaceous, a considerable series of forms being known from all of the principal marine horizons representing this division of geologic time. We find the Ichthyosauria as a group showing a remarkable unity with a fairly direct tendency of evolution marked out in all the subdivisions, and a considerable number of stages are passed through in the known history. It is therefore to be expected that to express the classification of the group in the form of phylogeny would be a fairly simple matter. In a general way the horizontal classification, *viz.*, that recognizing the forms of only one horizon, meets few obstacles. In a linear arrangement the tendency of progression, specialization, or evolution is distinct, and the stages recorded are fairly definite. In viewing the whole scheme both horizontal and linear it is, however, difficult to discover characters which are fundamental and persistent, or which are adaptive and persist unchanged to such a degree that they may be used in a classification scheme. To a certain extent it is true that in passing from one period to another the characters considered as diagnostic are replaced by others.

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[41] Gilmore, C. W., Mem. Carneg. Mus., vol. 2, no. 2, and no. 9.

[42] Andrews, C. W., Geol. Mag., Dec. 5, vol. 4, p. 202.

The characters on which the classification of the Ichthyosauria was based by Baur included only modifications of the extremities and dentition, both of them features which would most readily respond in adaptation to aquatic conditions. The distinguishing characters of the Shastasauridae as originally described were found in the "peculiar articulation of the dorsal ribs, the form of the pelvic arch, and the presence of the long-spined chevrons." It has been shown more recently that the type of limb structure in *Shastasaurus* is also quite different from that in the other divisions of the Ichthyosauria.

Of the various groups of characters in which the Ichthyosauria show differences, the strongest contrasts are found in the (1) limbs, (2) pelvic arch, (3) caudal fin, (4) caudal chevrons, (5) articulation of dorsal ribs, and (6) the dentition. The variation in most of these characters may apparently be attributed to adaptation of the peculiar type expressed in the Ichthyosauria.

If the ichthyosaurs be taken as a whole, one of the most striking contrasts is shown in a comparison of the Triassic and post-Triassic forms, particularly in the characters just mentioned, as is indicated by the following table:

	TRIASSIC						JURASSIC CRETACEOUS		
	Cymbospondylus	*Mixosaurus*	*Merriamia*	*Delphinosaurus*	*Shastasaurus*	*Toretocnemus*	*Ichthyosaurus*	*Baptanodon*	*Ophthalmosaurus*
Rib articulation mainly single	x	x	x	x	x				
Rib articulation mainly double						x	x	x	x
Distal end of caudal series strongly decurved			?		?	?	x	x	?
Caudal vertebrae with Y-shaped lower arches	x	x	?	x	x	x			
Pelvis plate-like, not reduced	x	x	?	x	x	x			
Pelvis much reduced							x	x	x
Scapula much broadened distally	x	x	x	x	x	?			
Epipodials separate and relatively long	x	x	x	x	x*	x			
Hyperphalangy developed							x	x	
Phalangeal elements sometimes shafted	?	x	x	?		x			
Phalanges polygonal or discoidal	?			?	x		x	x	x
Phalanges reaching double the normal formula for diapsidan reptiles	?			?	?		x	?	
Teeth numerous	x		x	?	?	?	x		
Teeth differentiated		x		?	?	?			
Teeth in pits	x*	x		?	?	?			

*In part.

Considered without regard to age, the dividing line in the Ichthyosauria would certainly be drawn between the well-known Triassic genera on the one hand, and on the other hand the post-Triassic *Ichthyosaurus* and later types. Considered from the historical point of view it might be presumed that as most of the characters in which these groups differ are closely connected with the peculiar kind of adaptation which we see here, the differences simply express stage of evolution; and that probably some of the known Triassic forms are ancestral to *Ichthyosaurs*, *Baptanodon*, and *Ophthalmosaurus*.

If the post-Triassic types be excluded from consideration, as presumably derived from some of the known Triassic forms, the contrasts shown in the remaining ichthyosaurs are much less marked. The principal contrasts seen in the Triassic forms are in the structure of the podial region of the limbs, in the rib articulation of the cervical and dorsal region, and possibly in the dentition. In

Mixosaurus the podial region is broad and forms a relatively large part of the paddle. In the American Upper Triassic genera, which are probably slightly younger than *Mixosaurus*, the corresponding region forms a relatively small portion of the limb. It is also relatively narrow and the number of digits is reduced. In *Cymbospondylus*, from an earlier Middle Triassic stage than *Mixosaurus*, the structure of this region is not certainly known, but the podial portion appears to have three transverse rows of phalanges like *Merriamia*, while the form of the distal end of the ulna suggests the presence of a fourth or posterior element in the proximal row of the mesopodial region as in *Mixosaurus*. In the rib articulation, *Mixosaurus* seems to be characterized by the presence of only a single head in the dorsal and cervical region, and a possible incipient division of the broad heads of the posterior dorsals and anterior caudals. In all of the American Triassic genera, excepting *Toretocnemus*, no division occurs in any part of the series excepting in the most anterior portion of the vertebral column, where it is always present. In *Toretocnemus* the middle dorsals show a wide division of the rib head. This seems to extend well back toward the pelvis. The anterior dorsal and cervical regions of this genus are unknown. The limb structure is apparently like that in *Merriamia*. In the specimens referred to *Mixosaurus* (?) *atavus*, the oldest known ichthyosaurian occurring in the Middle Trias, both single and double articulations occur, and two distinct types may be represented.

On the basis of difference of limb structure and rib articulation, *Mixosaurus* would apparently be separated from all of the American genera as a broad-paddled, pentadactyl type, in which bicipital rib articulation is reduced to a minimum. The American genera including *Toretocnemus* would be distinguished as narrow-paddled and with persistent bicipital rib articulation in the cervical region. *Toretocnemus* might be classed with the American shastasaurines as a form in which the limb structure had become narrowed or leptocheirous, but in which an original bicipital rib articulation had persisted. The European *M.* (?) *atavus* may be in part related to *Mixosaurus*, and in part to other groups with bicipital rib articulation.

It is doubtful whether any single group of characters should be used in attempting to determine the course of development or the relationships of the forms in this order. We may, however, fix upon those features which have been most persistent, and have generally followed the most direct course of evolution. The most persistently differing characters in close relation to adaptation are found in the variation in structure, and possibly in function of the paddles. This variation is apparent from the Triassic forms up to the acme of the Jurassic representatives of the group. The most marked difference in characters which might be considered as fundamental is found in the rib articulation. Both the broad and narrow types of paddles are far removed from a primitive form of the limb. While the rib articulation has evidently also varied considerably in all of the forms, it is to be presumed that in certain parts of the vertebral column the characters have changed less than in the limbs, which are in closer touch with the environment.

If an attempt be made to classify all of the ichthyosaurian groups on the basis of the structure of the paddles or of the rib articulation, it is seen that the characters do not vary together. They are so entangled that broad and narrow types of paddles appear in forms with mainly bicipital articulation, as in the latipinnate and longipinnate forms of *Ichthyosaurus*, and are also found in types with mainly single articulation as in the broad-paddled *Mixosaurus* and the narrow-paddled *Merriamia*. If therefore any phylogenic scheme is to be based on these characters, it will be necessary to determine which of these two kinds of variation is the more primitive, and which has developed secondarily in the separate lines of descent. Of the two sets of characters, the nature of the rib articulation would seem to be more nearly fundamental than the structure of the paddles; and one of the forms of rib articulation is presumably primitive, the other being a variation from it.

From evidence which has been presented in the general discussion of the vertebrae (p. 270) there seem to be some reasons for considering the double articulation as more probably primitive than the single articulation. If such be the case, all Triassic forms excepting *Toretocnemus* and *M.* (*?*) *atavus* must be set aside as specialized and not ancestral to *Ichthyosaurus*. If the double articulation be primitive, the forms with bicipital articulation, as *Ichthyosaurus* and *Baptanodon*, have retained a primitive character not preserved in the shastasaurines or in *Mixosaurus*, and these groups must be considered as specialized branches from the persistent stock, and not ancestral to *Ichthyosaurus*.

On the other hand, if the single articulation of the rib head be primitive, *Mixosaurus* may lead directly toward *Ichthyosaurus*, though the American forms would still remain as a separate group, excepting possibly *Toretocnemus*. This last genus, in spite of the presence of what is considered a primitive character, is geographically so situated as to make its relationship to *Ichthyosaurus* very doubtful, and the similarity of its limb structure to that of *Merriamia* makes it probable that it is to be considered as a persistently primitive form coming from the same stock as *Merriamia*.

If the double rib articulation be primitive, there is as yet no form known which would be considered as the ancestral ichthyosaurian type, unless it be one of the imperfectly known forms of *M.* (?) *atavus* of Europe. If for no other reason, the geographic situation of this type, which is itself a factor in classification, is such as to suggest that *Ichthyosaurus* is descended from it, and that *Mixosaurus* is also derived from it. Whether the American genera can be considered as derived from *M.* (?) *atavus* or from some earlier form must be left undetermined until more is known of *M.* (?) *atavus*. As yet the available material is very scanty. The geographic situation of *M.* (?) *atavus* is also very distant from that of the oldest American Middle Triassic forms, and the disparity in age is not great; so that the ancestors of the American forms may have come from some region other than Europe.

Without being able to construct a thoroughly satisfactory phylogenic scheme, there appears to be good reason for considering that there are present in the known material representing this order, at least four groups in which the common origin of the constituent members is fairly certain, and in which the rank of the larger included groups is high enough so that the four divisions must themselves be considered as not ranking lower than subfamilies. These divisions are the Ichthyosauridae, Baptanodontidae, and Mixosauridae of Baur, and the Shastasauridae of Merriam. Of these groups the Ichthyosauridae and Baptanodontidae are both types with bicipital articulation of the dorsal ribs. They are otherwise closely related, and may be brought together as one group, which might well be designated the Ichthyosauridae with two divisions. If *Ichthyosaurus* is divided into several genera as is the present tendency of writers, and if *Baptanodon* is to be distinguished generically from *Ophthalmosaurus*, this family should be subdivided into two subfamilies, the Ichthyosaurinae and Baptanodontinae.

The relation of the American shastasaurs to the mixosaur group is not entirely clear, but the character of the dorsal rib articulation and the general correspondence in other parts of the skeleton suggest that the resemblance may mean more than primitiveness alone, and that these two divisions should be united in a larger group of family rank, the Mixosauridae, with the Shastasaurinae and Mixosaurinae as subdivisions.

The following arrangement seems most nearly to represent the relations of these groups:

Ichthyosauria

- Mixosauridae
  - Mixosaurinae
    - *Mixosaurus*
  - Shastasaurinae
    - *Cymbospondylus*
    - *Merriamia*
    - *?Toretocnemus*
    - *Delphinosaurus*
    - *Shastasaurus*
- Ichthyosauridae
  - Ichthyosaurinae
    - *Ichthyosaurus*
  - Baptanodontinae
    - *Baptanodon*
    - *Ophthalmosaurus*

In this arrangement *Toretocnemus* is placed with the Shastasaurinae as a type in which the rib articulation has remained more primitive than in the others, or has been secondarily divided in the posterior dorsal region. *M.* (?) *atavus* may be associated with either of the two families; it may be subdivided into two quite distinct groups and associated with both; or it may be considered ancestral to both.

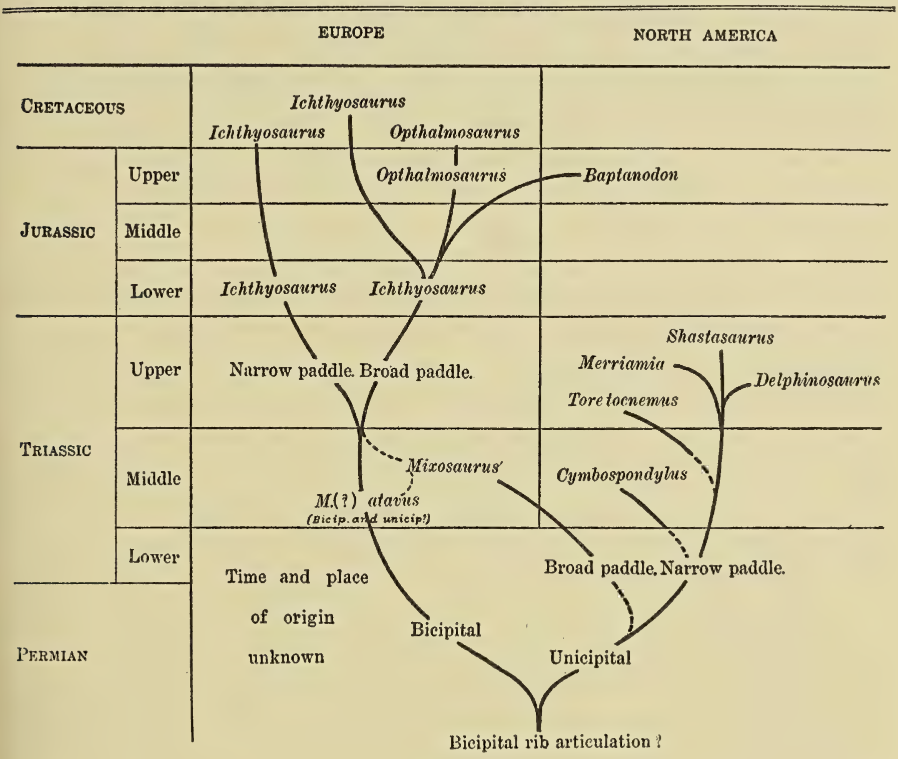
The phylogenetic scheme on the following page illustrates the broader relationships of the ichthyosaur groups, as they may be assumed to be situated on the basis of a primitive bicipital rib articulation.

The major divisions of the Ichthyosauria may be defined as follows:

Ichthyosauria

Mixosauridae

Articulation of dorsal ribs generally unicipital. Hypocentral elements of the caudal region uniting to form long-spined chevrons. Distal region of caudal series not strongly decurved. Zygapophyses in anterior half of vertebral column consisting of distinctly separated lateral faces. Number of presacral vertebrae may reach 65. Pelvic elements plate-like, relatively large. Scapula expanded distally. Epipodial elements relatively elongated, and separated by a cleft (excepting in *Shastasaurus careyi*). Hyperdactyly not developed. Hyperphalangy less marked than in Ichthyosauridae. Phalangeal elements frequently elongated and shafted. Facial region shorter and maxillary longer than in Ichthyosauridae. Orbits relatively small in most forms. Postorbital bar not markedly narrowed. Teeth few to numerous, isodont or differentiated, in open grooves or in pits.


EUROPE
NORTH AMERICA
CRETACEOUS
JURASSIC
Upper
Middle
Lower
TRIASSIC
Upper
Middle
Lower
PERMIAN
Ichthyosaurus
Ichthyosaurus
Opthalmosaurus
Opthalmosaurus
Baptanodon
Ichthyosaurus
Ichthyosaurus
Narrow paddle.
Broad paddle.
Mixosaurus
M.(?) atavus
(Bicip. and unicip?)
Shastasaurus
Merriamia
Delphinosaurus
Tore tocnemus
Cymbospondylus
Broad paddle.
Narrow paddle.
Time and place
of origin
unknown
Bicipital
Unicipital
Bicipital rib articulation ?

Mixosaurinae. Presacral vertebrae 48–50 (?). Cervicals with unicipital rib articulation (?). Distal region of caudal series curved upward anterior to the posterior end, and slightly decurved distally; neural spines elongated and erected in the region of curvature. Pubis without obturator notch or foramen. Interclavicle with expanded median stem. Podial portion of paddles relatively long and broad, five digits present. Orbits moderately large. Teeth well spaced, set mainly in pits, differentiated.

Shastasaurinae. Presacral vertebrae 45 (?) to 65. Cervicals with bicipital rib articulation. Distal region of caudal series as in the Mixosaurinae, or somewhat decurved as in the Ichthyosauridae. Pubis with obturator notch or foramen. Paddles with relatively short and narrow podial region. Digits where known reduced to three or four. Orbits small to large. Postorbital bar not greatly narrowed. Teeth numerous, close set in open grooves or in pits.

Ichthyosauridae

Articulation of the presacral ribs mainly bicipital. Hypocentral elements of the caudal region sometimes absent, when present not meeting to form long-spined chevrons. Distal portion of caudal series sharply decurved and enclosed in the lower portion of a two-lobed sculling fin. Zygapophyses consisting of a single anterior or posterior face. Presacral vertebrae about 45 in number. Pelvic elements much reduced. Scapula narrow distally. Hind limbs generally much reduced. Epipodial elements very short and not separated by a cleft.[43] Hyperdactyly frequent. Hyperphalangy very pronounced. Phalangeal elements polygonal or rounded. Facial region relatively long. Maxillary relatively short. Orbits very large. Postorbital bar generally narrow. Teeth numerous, isodont, in open grooves.

Ichthyosaurinae. Hypocentral caudal elements usually present.[44] Inferior pelvic elements separate or fused. Epipodial region of anterior limbs including only two elements.[45] Epipodial bones angular in outline. Phalangeal elements polygonal, sometimes notched on the anterior side in the anterior row. Teeth numerous.

Baptanodontinae. Hypocentral elements reduced, or absent from caudal region. Ilium and ischium fused. Epipodial elements three in number in the anterior limb. All limb elements excepting the propodial and anterior epipodial are discoidal in form, and with excavated or pitted margins. Orbits very large, and postorbital bar very narrow. Teeth few and small.

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[43] Very exceptionally slightly separated.

[44] See page 260.

[45] Rarely, as in *Ichthyosaurus extremus*, with more than one element.

SYSTEMATIC DESCRIPTIONS

Mixosaurus (?) *atavus* (Quenstedt)

Ichthyosaurus atavus Quenstedt, Petrefactenkunde, Aufl. I, 1852, p. 129; Aufl. II, 1867, p. 160, Taf. 6, fig. 7–10.

Mixosaurus atavus, *major* and *minor* (Fraas), Ichthyosaurier d. Süddeutschen Trias- und Jura-Ablagerungen, 1891, p. 37, Taf. 1, fig. 17 and 18; Taf. 3, fig. 1–16.

Ichthyosaurus (?) *atavus* (Merriam), Am. Jour. Sc., vol. 19, p. 30, Jan., 1905.

To this species Quenstedt referred a number of fragmentary Triassic specimens evidently representing ichthyosaurians. In the absence of distinguishing characters it was included in the genus *Ichthyosaurus*. In additional material of similar type Fraas recognized characters separating this form from *Ichthyosaurus*, and included it in the genus *Mixosaurus*, which had been described by G. Baur from a study of the Italian Triassic material. More recently Merriam has questioned the generic identity of this form with the species referred to *Mixosaurus*.

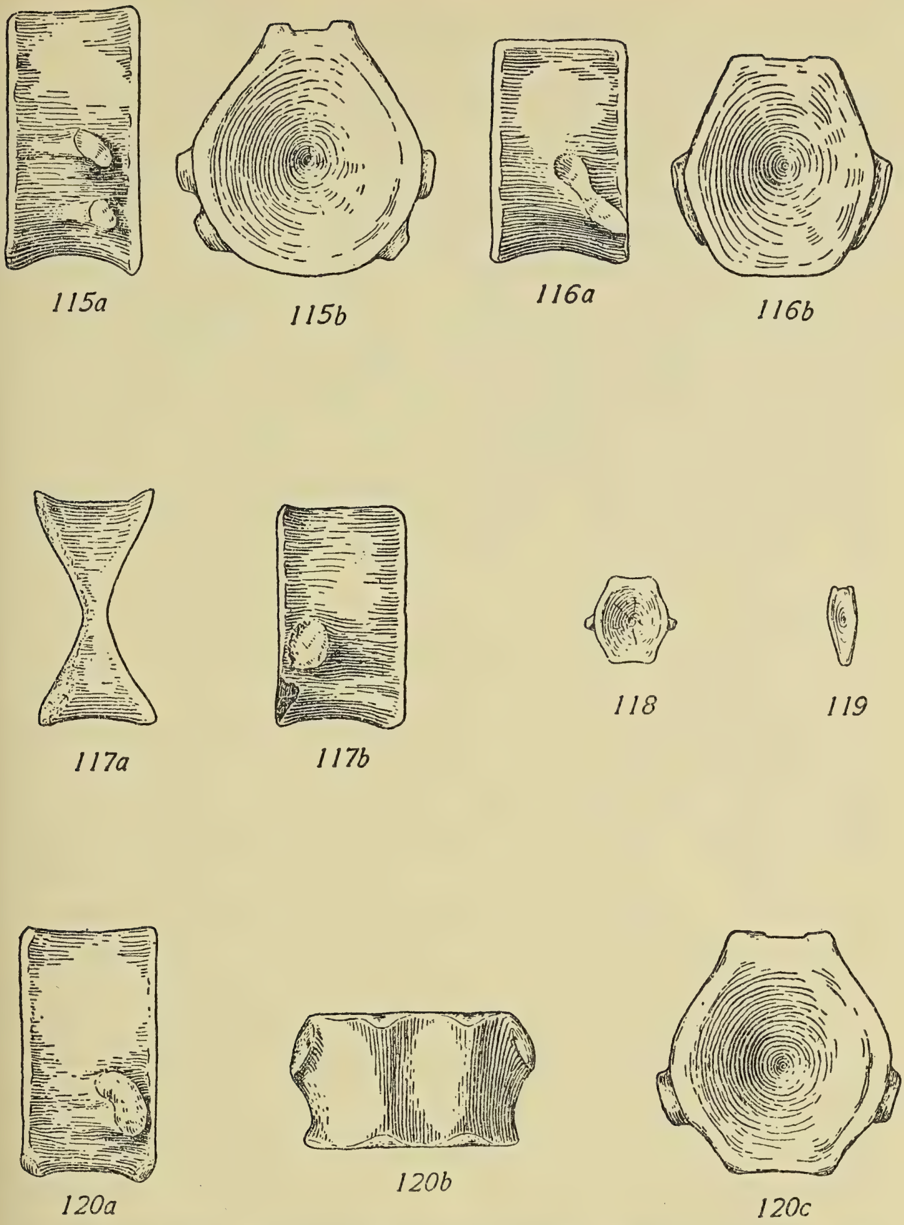
Vertebral Column.—The vertebrae of this form are known through a comparatively few specimens, nearly all of which are represented by centra without arches.

In the collection of the Königlichen Naturalien-Cabinet of Stuttgart there is a small centrum which, as far as can be determined, agrees in all its characters with the most anterior dorsal or cervical centra of *Ichthyosaurus* or *Cymbospondylus*. It is somewhat broader than high, and apparently had two lateral facets for rib articulation (fig. 61). The upper portion of the vertebra is however damaged so that the complete separation of the facets cannot now be proved. The upper facet was evidently continuous with the superior surface for articulation with the neural arch. A somewhat broken centrum, no. 3068, in the collection of the Polytechnikum of Zürich seems also to belong in this region, as the superior articulation with the rib is continuous with the articular surface for the upper arch. Part of the lateral face of the vertebra was unfortunately covered with matrix. This centrum is nearly circular in cross-section. The one from the Stuttgart collection has nearly the same form, but is a little broader, indicating probably a position near the posterior end of the cervical region.

There are no vertebrae available which represent the middle dorsal region, unless possibly a specimen (fig. 62) figured by Fraas (1891, Taf. 3, fig. 12) belongs there. This last vertebra is a very little higher than wide and seems to bear a single small apophysis just above the middle. The writer has not seen so small an apophysis for unicipital articulation of dorsal ribs in any ichthyosaur, but apophyses for rib articulation, of this size and similarly situated on the side of the centrum, are found in the middle tail region. The width of the centrum is, however, greater than is generally seen in caudal centra of Triassic genera and the inferior surface seems to show no facets for chevrons. Fraas considered this centrum a caudal. If it is not a caudal, it might possibly be considered as an anterior dorsal in which the tubercle of a widely-forked rib head rested entirely on the base of the upper arch.

Several vertebrae differing considerably in their characters seem to represent the posterior portion of the dorsal region. Of these the larger number are like figures 63, p. 265, and 115*a* and 115*b*. The first of these two specimens was described by Fraas, the second is from the collection at Zürich. The form of the first centrum and the inferior position of the apophyses can probably indicate no other position in the column than that near the pelvic region. The inferior surface is rounded, showing no facets for hypocentra, and it is evidently not a caudal but a posterior dorsal. Other centra including one (figs. 116*a* and 116*b*) from the collections at Zürich, and two from the collections of the Technische Hochschule of Stuttgart show a form of the centrum somewhat similar to those just described, but support only a single lateral apophysis. There are in these specimens no distinct traces of facets for intercentra, and it is not probable that they were situated far behind the pelvic region.

The first indication seems to be that the forms of centra discussed above show bicipital rib articulation in the dorsal region in one case and unicipital articulation in the other. That forms of articulation as different as these occurred in the same region of the vertebral



115a 115b 116a 116b

117a 117b 118 119

120a 120b 120c

FIGS. 115*a* to 120*c*. *Mixosaurus* (*?*) *atavus* (Quenstedt). All figures natural size. Figures excepting 118 and 119 from rough sketches by the author.

FIGS. 115*a* and 115*b*. Posterior dorsal vertebra showing double rib articulation. From the collections of the Polytechnikum, Zürich.

FIGS. 116*a* and 116*b*. Posterior dorsal showing single rib articulation. From the collections of the Polytechnikum, Zürich.

FIGS. 117*a* and 117*b*. Posterior dorsal showing double rib articulation. From the collections of the Polytechnikum, Zürich.

FIGS. 118 and 119. Caudal vertebrae. (After Fraas.)

FIGS. 120*a* to 120*c*. Anterior caudal vertebra showing facets for chevrons. From the collections of the Polytechnikum, Zürich.

column in variations of the same specific or even generic type seems improbable. It appears that we are dealing either with different parts of the vertebral column of similar individuals, or with quite different types occurring together, like *Toretocnemus* and *Merriamia* in the Upper Triassic of California.

With some evidence of double articulation in the anterior dorsal region and also in certain posterior dorsals, it is possible that all ribs back to the pelvis were double-headed, and that the vertebrae possessing a single large lateral apophysis, but without facets for lower arches, were in the pelvic region or immediately behind it.

If it should be shown that figure 62, page 265, really represents a type with unicipital middle dorsal ribs it is probable that there are two types represented, one with mainly or entirely single-headed ribs and the other with double-headed ribs back at least to the pelvis.

In neither case does there seem to be evidence that there are double rib articulations in the caudal region, behind vertebrae to which single-headed ribs are attached.

A typical vertebra from the anterior portion of the caudal region is represented in figures 120*a*, 120*b*, and 120*c*. The centrum shows some lateral compression and has a hexagonal cross-section. The inferior surface presents prominent angles on which distinct facets for the inferior arches are present. Other posterior caudals, one of which shows a high degree of lateral compression, are represented by figures 118 and 119 (Fraas, 1891, Taf. 3, figs. 15*b* and 16*b*).

Most of the forms of vertebral centra seen in the specimens described above do not correspond exactly to those of other ichthyosaurians. In those with double-headed rib articulation the heads seem to have been more widely separated in the posterior dorsal region than in *Ichthyosaurus*. This may indicate a more primitive stage of a reptilian form originally with double-headed ribs, from which *Ichthyosaurus* is derived. The centra in which the position in the vertebral series has been determined by the form of the cross-section, and by the confluence of the upper portion of the rib articulation with that for the upper arch, are much like cervicals of *Ichthyosaurus*, *Shastasaurus*, or *Cymbospondylus*. In the centra with single articulation in the pelvic region the form is not very different from that in *Cymbospondylus*. If the specimen represented in figure 62, page 265, is a middle dorsal it is different from any other form known, but would apparently approach nearer to *Mixosaurus* than to any other genus.

As far as has been observed the centra of all of the vertebrae of the *M.* (?) *atavus* type are deeply biconcave and do not show a marked flattening of the anterior and posterior faces near the periphery (figs. 117*a* and 117*b*). An exception may appear in some of the distal caudals.

Of the vertebral arches the only one known to the writer is the upper arch (figs. 34*a*–34*c*) described by Fraas (1891, Taf. 3, figs. 6*a*–*c*). This is an anterior dorsal arch of much the same type as in *Cymbospondylus*. The zygapophysial facets are very primitive in that they are still distinctly separated, they do not fall into the same plane, and they are still far from coming into a horizontal position.

Limb and Arch Elements.—The only limb bones of *M.* (?) *atavus* known include a humerus described by Fraas (1891, Taf. 3, fig. 5), and several separated podial elements figured by Quenstedt (1852, Taf. 6, figs. 9–10). The humerus is a slender but not greatly elongated element with a very high pectoral ridge. Though somewhat damaged distally it does not appear to be more slender than the propodial element in a number of other ichthyosaurians (see von Huene 1902, p. 11). The other known limb elements are possibly mesopodials.

A number of bones from the arches are known but have not yet been described.

Jaws and Dentition.—Of the skull only a few fragments consisting of jaws are described. Excepting the somewhat greater prominence of the surface sculpture, and the insertion of the teeth, these elements are much as in *Ichthyosaurus*.

The dentition which is fortunately known in several jaw fragments presents interesting characters which suggest that *Mixosaurus* is possibly a closely related type. In the several specimens which Fraas had before him there were present a portion of an anterior end of a jaw with slender conical teeth (fig. 15, p. 238) and a part of a jaw in which there are two teeth with low blunt crowns (fig. 16, p. 238). In one of the two teeth in the second fragment the crown is considerably compressed laterally, and is a little lower than in the other. In both teeth the crown shows surface markings on the enamel, and is apparently not reduced by wear. The bases exhibit strong folds of the dentine, and appear to be partly in pits.

These specimens apparently indicate a differentiated dentition similar to that seen in *Mixosaurus*. The structure and insertion of these teeth are somewhat like that of the ichthyosaurians described from the Trias of Spitzbergen (see p. 383).

Mixosaurus Baur

Ichthyosaurus (Bassani), Atti della Soc. Ital. di Sc. Nat., vol. 29, p. 15.
Mixosaurus Baur, Amer. Naturl., vol. 21, 1887, p. 839.

Distal end of caudal region slightly bent but not sharply decurved as in *Ichthyosaurus*, broadened by elongation and erection of the vertebral arches. Caudal vertebrae with Y-shaped chevrons. Rib articulation mainly single-headed, with a disposition to divide indistinctly shown in the posterior dorsal and anterior caudal regions. Inferior pelvic elements plate-like. Interclavicle tending to assume a triangular rather than a T-shaped form. Anterior limbs and arches considerably larger than posterior. Humerus not relatively elongated compared with *Ichthyosaurus*, in some instances much abbreviated or broadened. Epipodial elements relatively elongated, radius with median constriction, ulna convex on posterior border. Digits five, maximum number of phalanges ten to eleven in the longest digit. Phalanges generally somewhat elongated and with median constriction or lateral notch. Elements of posterior limbs generally less specialized than those of anterior limb. Skull relatively large compared with size of trunk. Facial region relatively short and maxillary relatively long compared with the form in *Ichthyosaurus*. Orbits large. Dentition showing some differentiation, anterior teeth slender-conical, posterior teeth blunt-conical. Teeth rather widely spaced, and set mainly in distinct pits.

The genus *Mixosaurus* was based by Baur on Bassani's *Ichthyosaurus cornalianus* of the bituminous shales in the Upper Triassic of Besano in northern Italy. Though material from other regions and other horizons has been referred to this genus, it is not certain that any of these forms really represent *Mixosaurus*. In the following discussion only the typical material from Italy is referred to this genus. The other forms may be doubtfully referred to this group or may be referred to other genera, as will be indicated elsewhere.

Known only from the Triassic.

Mixosaurus cornalianus (Bassani)

Ichthyosaurus cornalianus Bassani, Atti della Soc. Ital. di Sc. Nat., vol. 29, p. 15.
Mixosaurus cornalianus (Baur), Amer. Naturl., vol. 21, 1887, p. 839.
Mixosaurus cornalianus (Repossi), Atti della Soc. Ital. di Sc. Nat., vol. 41, p. 7.

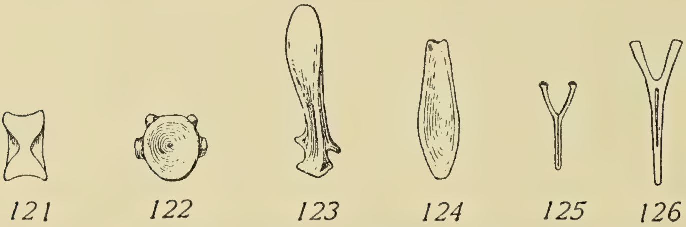
The material representing this species now in the Civic Museum of Milan includes a number of very excellent specimens, well illustrating the structure of nearly all of the important parts of the skeleton. The descriptions of Bassani and Baur having given only a suggestion of the characters present in this interesting animal, Dr. E. Repossi (1902) has made a satisfactory comparison with this material possible, through the publication of a number of excellent figures accompanied by a general description of the skeleton.

The specimens known are mostly small forms only a few feet in length. There are a few remains of larger individuals, but the average size of the forms is small compared with most other known ichthyosaurian groups. In contrast with *Ichthyosaurus* of the Jurassic, *Mixosaurus* shows decidedly less of the extreme specialization in adaptation to aquatic life. Although not only a typical aquatic form, but already far advanced along this line of specialization, in nearly all respects in which comparison can be made, it is decidedly more like a shore animal than are the Jurassic ichthyosaurs. This incompleteness of adaptation is seen particularly in the organs of locomotion, but is also expressed more or less distinctly in other portions of the body. Though *Mixosaurus* is probably not more primitive than the Middle Triassic Ichthyosauria of America, it is evidently one of the most generalized members of the group.

Some characters in which *Mixosaurus* departs from the typical ichthyosaurs possibly represent specializations of this particular genus rather than persistent primitive characters. The uniformly small size, in itself a primitive character, has however tended to keep the North-Italian forms more generalized in certain respects than some of the larger forms of the American Trias.

Vertebral Column.—Several of the best specimens taken together represent practically the whole of the spinal column, though in most specimens it is hardly possible to obtain thoroughly satisfactory information concerning all regions of the series. According to Repossi, the vertebral column consists of about one hundred to one hundred and five vertebrae. Judging from his figure (1902, tav. 8, fig. 1) of a nearly complete specimen there were between forty-five and fifty presacrals. In one of the Milan specimens the writer has counted about seventy-six vertebrae behind the posterior limb. These two estimates would seem to bring the total number up to one hundred and twenty. The number of presacrals appears approximately the same as that in *Ichthyosaurus*, though a complete specimen might show a few more than the average for the later genus. This is in strong contrast to the presacral formula of *Cymbospondylus*, which comprises more than sixty-five vertebrae.

As in all other ichthyosaurians the centra are biconcave. The concavity appears to extend well out toward the margins (fig. 121), and is not expressed mainly near the middle of the centrum, excepting possibly in the caudals.



Figs. 121 to 126. *Mixosaurus cornalianus* (Bassani). Figs. 121 to 125, after Repossi. Fig. 126, from rough sketch by the author. Figs. 121 to 125, natural size. Fig. 126, about natural size.

Figs. 121 and 122, dorsal vertebrae; fig. 123, neural arch of a dorsal vertebra; fig. 124, caudal centrum; figs. 125 and 126, lower arches of caudal vertebrae.

Throughout the larger part of the column, back to the middle of the caudal region, the neural spines are relatively high and slender, but are not greatly broadened anteroposteriorly. The zygapophyses are distinctly developed (fig. 123), but are not particularly large or strong. The writer is uncertain as to whether the zygapophysial facets are separated.

In the characters of the caudal region *Mixosaurus* differs greatly from *Ichthyosaurus*, and to a considerable extent indicates less complete adaptation to aquatic conditions. In its broader outlines the tail seems to differ considerably from the caudal region of all later Ichthyosauria. In contrast to the form of caudal fin seen in *Ichthyosaurus*, in which the distal portion of the vertebral column is rather sharply deflexed, the *Mixosaurus* specimens available show near the end a gentle upward curvature of the column, which then bends down again and straightens out near the distal portion. (See fig. 45, p. 255, and fig. 50, p. 257.) The structure seen here would evidently offer support to a distal expansion of the tail, and would considerably increase its power beyond that of the form of propelling tail which is commonly found in types which inhabit both shore and water. This fin would possibly have less power than the wider expansion of the double-lobed fin of the typical *Ichthyosaurus*. Evidently the form seen here marks the transition from the straight, but somewhat broadened, tail of a shore dweller to the specialized fluke of the later ichthyosaurs.

As has been shown by Repossi (1902, tav. 9, fig. 8), the superior arches of the caudal vertebrae near the bend in the tail are extraordinarily high, and tend to take an erect position; those over the posterior portion of the bend inclining forward. This peculiar feature is noticed in those exhibition specimens in Milan in which the caudal region is well shown. Its function is evidently the broadening of the caudal fin at the point where the greatest amount of power can be applied to the best advantage. It is paralleled in several other groups of aquatic saurians in which the adaptation has been generally considered somewhat less complete than in the ichthyosaurs. In the mosasaurian genus *Clidastes* the relations of this portion of the tail region are somewhat similar. (See fig. 51, p. 258.)

In addition to increase of the height of the tail through the elevation of the superior arches we find the centra of a considerable portion of the tail region very much compressed laterally and relatively high (fig. 124).

As in the American Triassic forms, the lower arches of the caudal region are united ventrally to form long-stemmed chevrons. The form of these chevrons is not unlike that in *Delphinosaurus perrini*. It is possible that Repossi's fig. 9*c*, tav. 9 (1902) represented as an upper arch is really a chevron, as it duplicates the form of chevrons shown in the specimens in the Milan museum. (See figs. 125 and 126.) It may be noted that the space available for the spinal canal is relatively much larger than in the large unquestionable neural arches figured by Repossi (1902, tav. 9, fib. 9*b*). The lower arches extend behind the bend in the tail and appear to be at least as long in that region as are the considerably shortened neural arches.

The nature of the inferior arches below the region in the tail in which the upper arches are elongated most is not clear. According to Repossi's representation of this region (1902, tav. 9, fig. 8), the facets for chevrons are much reduced or absent here. The inferior arches sketched in dotted lines in Repossi's figure do not actually exist in the specimen. On another specimen in which the caudal region is otherwise well shown, the hypocentra are again absent from this region. Though lower arches are present farther back in the tail, it is possible that they became reduced below the region of upward curvature.

Ribs.—In contrast to the bicipital articulation in the typical ichthyosaurs, the heavy ribs of the dorsal region articulate on a single head (see fig. 60*a*, p. 264), as has been shown by Repossi. In the cervical region the rib articulation seems to be single-headed as in the dorsal region. On one specimen a short rib, apparently belonging to the third or fourth vertebra behind the skull, has a single head. As interpreted and figured by Repossi, the ribs of the posterior dorsal or lumbar vertebrae are double-headed.[46] In discussing this peculiarity of *Mixosaurus*, Yakowlew (1902, 1 and 2) has suggested that as the single-headed rib precedes the double-headed in the history of the Ichthyosauria, the latter form is evidently to be derived from a single articulation by some process of division of the rib head. Since this division seemed to appear first in the pelvic region of *Mixosaurus* the suggestion was made that its appearance was connected with the extraordinary movements of this portion of the body in the use of the tail as a sculling organ. The relations of the ribs of *Mixosaurus* as described being entirely different from those of the American forms, in which a double articulation occurs in the neck only, the writer has examined, as carefully as possible, the excellent specimens on exhibition in the Milan museum, for evidence bearing on this point. This examination shows that in some cases at least the short ribs near the pelvic region or the base of the tail have broad undivided heads, as in the shastasaurian forms of the American Trias. In other instances ribs belonging to the anterior caudal region seem actually to show a beginning division of the articular face. In one case where the evidence seemed strongest, the apophysis on the vertebral centrum showed also some indication of division. It should, however, be noted that even in this instance the evidence hardly appears to warrant a definite statement that double articulation occurs, as the side of the vertebral centrum is badly broken up, and does not present a satisfactory case. The heads of these ribs are, moreover, not fully exposed, and it is not impossible that careful preparation with a needle will show that the apparent gap between the two rib heads is filled by a bridge of bone, now covered by matrix lying in a lateral groove. It is also worth noting that with the form which these ribs appear to have as they lie in the matrix, the upper head could not come into direct articulation with the diapophysis without elevating the shaft above the level of the other ribs.

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[46] Through a typographical error the original descriptions did not agree with the figures.

Though it is difficult to make certain of the identity of all of the specimens which have been described by Repossi, it has appeared to the writer that the most strongly forked rib figured by him (1902, tav. 9, fig. 10) possibly corresponds to a cross-section of a certain neural arch which is associated with other specimens that have evidently been the originals for some of his excellent figures of vertebrae and ribs.

On the whole, the few instances in which bifurcation of the articular heads of ribs may occur seem to the writer to be not sufficiently clear to warrant a definite statement that these ribs are normally divided, though a tendency in that direction may possibly exist. On the other hand, that such a disposition to divide should exist is rather remarkable when we consider that the American Triassic forms show an evident tendency to lose the bicipital articulation, and that they retain it only in the anterior vertebrae. In the typical *Ichthyosaurus* and in *Baptanodon*, where double-headed ribs are well developed through the greater part of the costal series, the pelvic and caudal regions are the only places where they do not normally occur.

Abdominal ribs are present in the Milan specimens of *Mixosaurus*. In Repossi's figures they resemble those of the American Triassic forms in the union of the pieces next the middle line of the abdomen to form a median spine, though the spine appears to be longer and more acute than in *Cymbospondylus*.

Extremities.—As was first shown by Baur (1887, 2), the limbs of *Mixosaurus* furnish fairly definitely evidence that the ancestral ichthyosaurian type was a shore form. In Baur's figure of the limb the characters of the propodial and epipodial segments were somewhat exaggerated, as the bones in this region are really less slender and relatively less elongated. In other portions of the limb, which were possibly not examined by Baur, other characters appear which also point definitely toward an ancestral form with a simple type of limb like that in a shore form. The characters emphasized by Baur are therefore not to be considered as incidental or accidental developments paralleling what is seen in an ambulatory type of limb, but they express in one way what is also definitely shown in other parts of the limb, or in the limb as a whole, and is distinctly visible in most other parts of the body.

Fortunately a number of the *Mixosaurus* specimens in the Milan museum are preserved in a fine shale, and as the individuals are small, the limbs have in some instances been buried almost entire before decomposition could permit a scattering of the elements. The figures of an anterior and a posterior limb shown by Repossi (1902, tav. 9, figs. 2 and 3) evidently represent almost perfect extremities. Contrary to what might have been expected from what is known of some other primitive Triassic ichthyosaurians, the posterior limbs are very considerably reduced in size below the dimensions of the anterior limbs. Evidently the hind limbs had already to some extent lost their usefulness, and were degenerating.

The *anterior limb* while considerably larger than the posterior one is also in some respects more specialized. In other words it has retained larger size as advantageous in the performance of its peculiar functions connected with locomotion by swimming. The hind limbs not being required in swimming as much as the fore limbs have gradually become reduced, but have not in the course of this reduction been forced to acquire as many new characters in adaptation to aquatic conditions. The anterior limb (fig. 127) is more primitive than that of the typical *Ichthyosaurus* in several important particulars: the epipodial elements are elongated and separated by a wide gap; the number of digits is the normal five; the phalangeal elements are less numerous than in most ichthyosaurs; in many cases the phalanges are relatively elongated and show a median constriction. The humerus of *Mixosaurus* does not show particularly primitive characters. Compared with most species of *Ichthyosaurus* it is a relatively short and broad element. The humerus figured by Repossi (1902, tav. 9, fig. 2), with the remainder of the limb, though a relatively wide bone is very much narrower than in certain other specimens in the Milan collection. In one specimen the width of the humerus equals more than two-thirds of the length. On the whole, the shortening of the humerus in *Mixosaurus* is fully as pronounced as in *Ichthyosaurus* or *Baptanodon*. In some cases it is almost as extreme as in some of the specialized ichthyosaurs of the shastasaur group. In one specimen showing what is apparently the lower side of the humerus a well developed pectoral ridge extends along about two-thirds of the length of the bone.

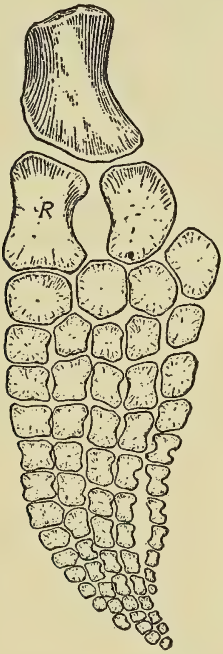

Fig. 127. *Mixosaurus cornalianus* (Bassani). Anterior limb, × ½. (Adapted from Repossi.)

In *Mixosaurus* hyperdactyly seems not to have developed, and hyperphalangy is not as far advanced as in *Ichthyosaurus*. The number of the phalanges is nevertheless far in advance of the normal, at least ten separate elements being present in the median digits. More strikingly primitive than the other characters of the digits is the tendency of particularly the proximal three to six phalanges of each digit to show an elongated form with a median constriction. In the distal phalanges, which are possibly added elements, the notches are less distinct or absent. As originally suggested by Lydekker for the notches on the margins of certain podial elements in the paddles of longipinnate ichthyosaurs, these notches or constrictions evidently indicate an original shafted form of the phalanges, which has been entirely lost in *Baptanodon* and in most of the late ichthyosaurs. The constriction of the phalangeal elements is in reality somewhat more strongly expressed on the specimens than it appears in Repossi's illustrations.

On one specimen where both fore and hind limbs are represented the *hind limb* appears to be less than two-thirds the size of the anterior one, and the bones of the pelvis appear correspondingly small. Both propodial and epipodial elements are here more slender and generally more primitive than in the anterior limb. (See fig. 97, p. 284). The phalanges are also more slender and seem not to have increased in number to such an extent.

In the first row of the mesopodial section of the hind limb figured by Repossi (1902, tav. 9, fig. 3), as in the anterior limb, four elements appear instead of three. (See fig. 111, p. 289.) The structure which appears in this case is unusual but is probably explained by another specimen (fig. 110, p. 289) in the Milan museum, in which only three elements are present in the proximal row. The lunate intermediate element in the second specimen almost closes the gap between the tibiale and fibulare, but in a second row of bones three elements articulate with the distal border of the intermedium; of these the anterior one has crowded up between the tibiale and intermedium so as almost to come in contact with the tibia. In the specimen figured by Repossi this element of the second row seems to have reached the tibia. This explanation not only accounts for the fourth element of the proximal row but may also explain the presence next the posterior border of tarsale one, and apparently functioning as tarsale two, of an element showing a strong median constriction. This constricted bone has the appearance of a metapodial or phalange, and if the explanation given above is correct it is really a metapodial moved upward into the position of tarsale two. This does not, however, explain the presence of lateral notches in other evident mesopodials shown in figure 110.

Limb Arches.—All four elements of the *pectoral arch* are figured by

Repossi. (See fig. 80, p. 276.) The coracoid and scapula are represented as almost identical in form. So similar are they that unless corresponding elements from the opposite side of the body are known, and show similar evidence as to relative position, these two bones might be suspected of being either two coracoids or two scapulae. Their form is not entirely similar to that of any elements in the pectoral arches of other ichthyosaurians.

The clavicle is slender compared with the corresponding element of *Cymbospondylus*. The median end in contact with the interclavicle is considerably expanded, but the middle and lateral portions are very slender. The median stem of the interclavicle is much more expanded laterally than in the other known genera, and gives to the element as a whole a nearly triangular form. In other ichthyosaurians the median arm is narrow and the element takes on the T form. From beds referred to the lower Muschelkalk, von Huene (1902, p. 11) has described a more robust and more nearly perfectly triangular interclavicle. (See fig. 81, p. 278.) The form of this element suggests its possible origin for the median plate in the stegocephalian pectoral arch.

Without more definite evidence as to their position it is not possible to make certain of the identity of the two inferior elements of the *pelvic girdle*. (See fig. 71, p. 273.) Neither element shows the obturator notch or foramen present in all of the other Triassic genera. As shown in the figure the bone labeled *Pu?* resembles the ischium of *Delphinosaurus*, but is also like the pubis of *Toretocnemus* minus the pubic foramen. The element *Is?* approaches the form of the ischium in *Toretocnemus* and *Shastasaurus*, and is also like the pubis of *Delphinosaurus* or *Shastasaurus* minus the anterior hook. Both inferior elements are much expanded, as in the other characteristic Triassic ichthyosaurian genera. The ilium is relatively short and is somewhat widened distally as in most of the Triassic forms. On the whole the pelvis shows as close a resemblance to that of *Cymbospondylus* as to that of any of the Triassic genera.

Skull.—The principal features of the cranium of *Mixosaurus* have been represented by Repossi, but as yet the individual elements have not all been described in detail. The skull is as a whole relatively large compared with the trunk. If any estimate can be made from the nearly complete specimen figured by Repossi (1902, tav. 8, fig. 1), the length of the skull equaled about 65 per cent. of the length of the trunk. In *Cymbospondylus* the length equals about 36 per cent.; in *Ichthyosaurus*[47] it may equal 80 per cent. The facial region is elongated and evidently slender, but is not developed proportionately as in the later ichthyosaurs. The superior narial openings are situated much as in *Ichthyosaurus*. The orbits are large, though possibly somewhat smaller than in *Ichthyosaurus*. The rostral region is formed largely of the premaxillaries, though the maxillaries are relatively larger than in most ichthyosaurs. Repossi's figures seem to indicate that the nasals are greatly expanded as in the other genera. A considerable number of sclerotic plates in the orbit show the existence of a large orbital ring. The elements of the posterior portion of the skull are not clearly shown.

The long and slender mandibular rami do not appear to differ materially from the jaws of *Ichthyosaurus*. In the coronoid region no distinct process is developed, but there is some indication of a flattened area on the superior margin as in *Cymbospondylus*.

Dentition.—In the characters of its dentition *Mixosaurus* seems to represent a peculiar ichthyosaurian type. As was shown in part by Baur, the dentition is characterized by the relatively small number of differentiated teeth set in the narrow alveolar margins. In an upper jaw figured by Repossi (see figs. 13 and 14, p. 237) there must have been about twenty to twenty-three teeth present. On a lower jaw there have been forty or more. In *Ichthyosaurus* Fraas places the number for long-jawed forms at about fifty teeth per jaw. In all of the specimens shown, the teeth are set in open order, particularly in the anterior portion of the jaws, where they may be separated by a space equaling from two to five or six times the diameter of the basal portion of their crowns. Many of the roots are in distinctly separated alveoli. The anterior teeth of both jaws are long and slender. Toward the back of the jaws the crowns become lower and their basal diameter increases somewhat. The most posterior crowns may have a basal diameter twice as large as that of the anterior teeth, and a crown only half as high. Repossi's figures do not indicate the presence of a large amount of cement on the roots, nor is there indication of folding of the basal portion of the dentine as in *M.* (*?*) *atavus*. The enamel of the crowns seems in some cases to be sharply striated.

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[47] *I. integer.* See Fraas E. 1891, Taf. 7.

Classification.—As yet only one species, *M. cornalianus*, has been described which can be referred with certainty to this genus. Most of the other forms which have been referred to *Mixosaurus* might with equal right be placed in some other genus. It is not improbable that some of the Italian specimens now available will be found to vary specifically from the type of Bassani's *cornalianus*.

Cymbospondylus Leidy

Cymbospondylus Leidy, Proc. Philad. Acad. Nat. Sc., vol. 20, p. 177, 1868.
Cymbospondylus (Merriam), Univ. Calif. Publ. Geol., vol. 3, p. 104, 1902.
Cymbospondylus (Merriam), Univ. Calif. Publ. Geol., vol. 4, p. 33, 1905.

Presacral region of vertebral column including about 65 vertebrae. Distal end of caudal region slightly decurved. Neural arches turned forward in region of curvature. Vertebral centra of distal caudal region much compressed laterally. Caudal vertebrae with Y-shaped chevrons. Rib articulation single-headed excepting in the anterior region of the vertebral column.

Anterior arches and limbs but little larger than posterior. Interclavicle unknown. Humerus, radius, and ulna relatively long and narrow, ulna and radius both with median constriction. Digits unknown. Inferior pelvic elements broad, plate-like. Femur somewhat more primitive than humerus.

Skull with narrow rostrum consisting in a large part of premaxillaries. Facial region relatively shorter than in *Ichthyosaurus*, and maxillary relatively larger. Orbits relatively small, postorbital bar broad, but without lateral temporal opening. Basioccipital with concave condyle. Dentition isodont. Teeth numerous, set in pits in some cases at least.

Known only from the Middle Triassic of the West Humboldt and New Pass ranges of Nevada.

Three species of *Cymbospondylus*, *C. petrinus*, *C. piscosus*, and *C. grandis* were described by Leidy from fragmentary vertebrae.

C. petrinus is represented by forms attaining a length of thirty feet or more. The anterior and posterior faces of the vertebral centra are sharply concave in the central region, but are nearly flat in the peripheral half of the face. The anteroposterior diameter of the dorsal centra is less than one-half of their height.

The single fragmentary specimen of *C. piscosus* represents a form smaller than the average of *C. petrinus*. The vertebral centra are relatively longer, their anteroposterior diameter equaling more than half of the height. The anterior and posterior faces of the centra are sharply and regularly concave from the periphery to the center of the face.

C. grandis was founded on a fragment of a caudal vertebra from the West Humboldt Range, and possibly represents a large individual of *C. petrinus*.

Fragmentary material recently obtained at New Pass, Nevada, is referred to a new species, *C. nevadanus*. It is distinguished mainly by the short and massive elements of the epipodial region of the hind limb.

Cymbospondylus petrinus Leidy

Cymbospondylus petrinus Leidy, Proc. Philad. Acad. Sc., 1868, vol. 20, p. 178.
Chonespondylus grandis Leidy, Ibid.
Cymbospondylus petrinus (Merriam), Univ. Calif. Publ. Geol., vol. 3, p. 106.
Cymbospondylus? grandis (Merriam), Ibid.

This species is the best known of the American Triassic ichthyosaurs, being represented by many individuals, which collectively exhibit the greater part of the skeletal structure. It occurs in the exposures of Middle Triassic limestones in the West Humboldt Range of Nevada. Closely allied to the typical *C. petrinus* is a form, *C. nevadanus*, which has been obtained in Middle Triassic limestones exposed at New Pass, twenty-eight miles west of Austin, Nevada.

C. petrinus is represented by individuals averaging over twenty feet in length. In one very large skull, no. 9954, which does not seem to be specifically separable from this form, the dimensions of corresponding parts are about 50 per cent. larger than in specimen 9950 of *C. petrinus*, in which the length was over thirty feet. The anterior portion of the rostrum of specimen 9954 is absent, but the remaining part of the skull is over five feet in length.

Skull.—The structure of the skull in this type is fortunately almost perfectly shown in specimens 9950 and 9913 from American Cañon (pls. 2–6). Other skulls, some of which are nearly as complete, show similar structure. In no. 9950 the skull is preserved intact, and has been almost entirely freed from the matrix with relatively little difficulty. Excepting a slight depression of the frontal region practically no distortion has occurred.

Though it is relatively primitive in many respects, the skull in this form is typically ichthyosaurian. Like the typical Jurassic genera, the facial region is relatively long and slender, the premaxillaries and nasals are very largely developed, the frontals are small or are largely covered by the nasals, the superior nares occupy a nearly median position, and a heavy sclerotic ring is present. In contrast to the later forms the maxillaries are relatively larger, the snout shorter, the orbits smaller, and the lateral temporal region broader anteroposteriorly. In these respects the skull is more primitive than any described form from a later period.

Compared with the length of the trunk the skull is relatively short. As nearly as can be estimated, the length equals a little more than one-third that of the dorsal region. The skull of *Mixosaurus* seems to be relatively much longer, equaling about two-thirds the length of the trunk, while in *Ichthyosaurus* the relative length may be as great as 80 per cent.

In this species the antorbital portion of the skull is elongated as a rostrum, which narrows gradually along practically the whole distance out toward the anterior end, though the diminution in width is less noticeable immediately beyond the anterior ends of the maxillaries. The rostral region represents about 60 per cent. of the total length of the skull, but is relatively shorter than in any other ichthyosaurian with which the writer has any acquaintance, excepting *Ichthyosaurus breviceps*, from the Lower Lias, in which the length is 55 per cent. The extent of the maxillary anterior to the orbit is relatively larger than in any other ichthyosaurian. It amounts to 48 per cent. of the length of the antorbital region in this form, while in *I. breviceps* with a somewhat shorter rostrum, in which one would expect to find the maxillary relatively long, it is less than 40 per cent.

The *premaxillaries* extend more than half the total length of the skull. For a little more than half of their length behind the anterior end of the rostrum they meet dorsally. Behind this point they are separated by the nasals. In specimen 9950 the posterior ends pass above the anterior ends of the superior narial openings, but do not appear to extend any distance below them as seems to be the case in most other ichthyosaurians. In another specimen (no. 9954) the superior narial opening is cut into the posterior part of the premaxillary to some extent. In the rostral region the premaxillaries are sculptured so as to produce a peculiar roughened surface.

The *maxillaries* are longer in specimen 9950 than in any other described ichthyosaurian, both in relation to the length of the cranium and to that of the rostral region. Almost if not quite half of the dentigerous margin of the upper jaw is situated on these elements. A large *lachrymal* is clearly defined on this and other specimens. In specimen 9954 it reaches forward to the posterior border of the superior nares.

The *nasals* are large and extend back over the frontals almost to the pineal foramen.

In the frontal region of *Cymbospondylus* the nasals seem to cover as large a portion of the *frontal* elements as in *Ichthyosaurus*. This might be suspected to be due in part to the displacement of the very thin posterior edges of the nasals, but the area exposed in preparation is probably nearly normal, since in several specimens prepared the border has always exhibited the same characteristically marked outline.

In contrast to the situation in *Ichthyosaurus* the large *pineal foramen* is surrounded mainly by the parietal instead of wholly or in a large part by the frontals. A prominent crest rises rapidly behind the anterior ends of the parietals reaching a very considerable elevation above the middle of the superior temporal openings. The pineal foramen is situated in the anterior portion of this crest, where it occupies such a position that it is directed partly upward and partly forward.

One of the most striking features of the skull in specimen 9950 (see pls. 2 and 6) is the relatively small size of the *orbit*, as compared with that of the later ichthyosaurs. The orbit as it appears in plate 2 is very slightly depressed, but the amount of overlap of the broken upper end of the jugal amounts at most to not more than twenty-five millimeters or a little more than one-sixth of the height of the orbit. In another specimen (no. 9913, see pl. 6) crushed laterally so that the height of the orbit would tend to be increased, the size of the orbit is also relatively small. In specimen 9950 the antero-posterior diameter of the orbit is about one-sixth the length of the skull, in spite of the fact that the rostral region is relatively short. In *Baptanodon* as figured by Gilmore[48] (see also fig. 5) the length of the orbit is only a little less than one-fourth that of the whole skull including the much elongated snout. The relative size of the orbit is particularly noticeable in comparison with the anteroposterior diameter of the lateral temporal region. The anteroposterior diameter of the lateral temporal area equals about 83 per cent. of the fore and aft diameter of the orbit in *Cymbospondylus* (no. 9950); in *Baptanodon* it appears to be less than 25 per cent.

The *jugal* is considerably expanded horizontally, and is comparatively thin vertically, its transverse diameter equaling more than twice its vertical thickness. Its vertical diameter below the middle of the orbit appears somewhat less than in *Baptanodon*, and less than in most forms of *Ichthyosaurus*. The posterior end reaches upward and backward to meet the quadratojugal above the inferior temporal notch.

The exposed portion of the *postorbital* appears to have an approximately triangular form, though its upper posterior portion may extend backward beneath the supratemporal as in *Shastasaurus*, and its anterior limits above the orbit are not clearly determined. No suture line between the *prefrontal* and *postfrontal* can be distinguished on any specimen examined, nor is there a line of demarcation observable between postfrontal and postorbital. The anterior end of the prefrontal is overlapped by the lachrymals and the nasals. The posterior end of the postfrontal extends back over the squamosal almost to the posterior end of the temporal region.

A well preserved *sclerotic ring* is shown in specimen 9913, and a complete, unbroken, and apparently undistorted ring in no. 9954. In each specimen a series of plates comprising one-half of the ring shows eight or nine plates, making a total of sixteen to eighteen. Owen counted seventeen in *Ichthyosaurus communis*, and Fraas gives the number as varying from fifteen to twenty in *Ichthyosaurus*. Gilmore finds but fourteen plates in *Baptanodon*, and Andrews gives the same number for *Ophthalmosaurus*. In specimen 9913 the inner or median portion of each sclerotic plate bends sharply around the equator of the eyeball and extends over the inner side of the eye showing a flattening of the eyeball similar to that described for

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[48] Gilmore, C. W., Mem. Carneg. Mus., vol. 2, pl. 8.

Ichthyosaurus by Owen[49] and for *Baptanodon* by Gilmore.[50] The sclerotic ring is smaller compared with the size of the skull than in any of the later ichthyosaurs. In specimen 9913 the greatest diameter of the slightly distorted ring is a little more than 10 per cent. of the total length of the skull. In no. 9954 the greatest diameter is less than 10 per cent. of the total length. In *Ichthyosaurus platyodon* and *I. breviceps* the ring is relatively 40 or 50 per cent. longer.

The lateral temporal bar of *Cymbospondylus petrinus* is always characterized by uncommon length anteroposteriorly. Its height is somewhat less than in most ichthyosaurs. Relative to the length of the cranial region it is much less elevated than in *Baptanodon.* Behind the jugal the inferior side of the temporal bar is sharply cut out so as to form with the slightly concave coronoid region of the mandible an elliptical opening with its long diameter extended anteroposteriorly. According to the suggestion of McGregor[51] the temporal bar originally enclosed a lateral temporal opening, which was closed through gradual anteroposterior compression of the bar, owing to the enlargement of the orbit. In this form the bar shows fully as much area on the side of the skull as in many reptilian forms possessing a lateral temporal fenestra. Though the temporal bar has probably been somewhat reduced by enlargement of the orbit, it seems very doubtful whether it ever really enclosed a lower temporal fenestra.

The *squamosal* bone is a triradiate element, as in other ichthyosaurs, one branch extending forward and outward along the outer border of the superior temporal opening, one forward and inward along the outer side of the posterior arm of the parietal, and one reaching down to meet the pterygoid on the anterior plate of the quadrate. In a lateral view of the skull the squamosal represents only a small part of the exposed area of the temporal bar, as the lateral anterior arms are largely covered by long posterior processes of the postfrontal, which reach almost to the upper posterior angles of the skull. The large *supratemporal* is apparently triangular, the acute anterior angle extending forward between the postorbital and postfrontal. The superior margin in contact with the squamosal and postfrontal forms a nearly straight line. The inferior border is in broad contact with the quadratojugal as in *Ichthyosaurus*. In *Baptanodon* this contact is very narrow, and the temporal bar is exceedingly narrow at this point. The *quadratojugal* extends downward almost to the articular surface of the quadrate and is covered above by the supratemporal. Inferiorly it reaches forward over the inferior temporal notch to meet the jugal. The lower side is considerably thickened a short distance above the border.

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[49] Owen, R., Liassic Reptilia, part 3, p. 103. London, 1881.

[50] Gilmore, C. W., Am. J. Sc., vol. 23, p. 194, 1907.

[51] McGregor, J. H., Mem. Am. Mus., vol. 9, p. 91.

The occipital region of this species (pl. 5, fig. 1) is less satisfactorily known than the other parts of the skull, as the difficulties of preparation have been relatively great. In specimen 9950 most of the elements of the occipital region seem to be in nearly their original position, but the exact form of some of the bones cannot be definitely determined. In specimen 9913 the skull has been broken through obliquely in the occipital region, and the structure of some of the elements is more clearly shown.

The *basioccipital* has a peculiar and characteristic form in that its articular face for contact with the atlas is deeply concave instead of convex as in *Ichthyosaurus*. In articulation the broad concave face of the basioccipital received the strongly convex anterior face of the atlas. In specimen 9950 the deep concavity on the posterior face of the basioccipital extends out to the lateral margins. Inferiorly the posterior end of the basioccipital is rounded, and is truncate downward and forward as if for the accommodation of a hypocentrum. On specimen 9913 the concave face extends almost to the lateral margins, and the inferior side of the concavity is bounded by a prominent lunate ridge, which tends to have somewhat the form of the spout-like odontoid process of the Ungulata. Below the prominent inferior ridge the inferior side is not truncated as in specimen 9950, but a sharply concave area extends around the lower side of the bone between the lunate ridge and the outer margin of the posterior side. The form of the posterior face of the basioccipital in specimen 9913 suggests that the concave face has been secondarily developed on a strongly convex face.

On the inferior side of the basioccipital there are situated two prominent apophyses similar to those on the inferior face of the basioccipital of *Sphenodon*.

The small and somewhat distorted *lateral occipitals* are seen in place in specimen 9950. They appear to be perforated or notched for the passage of nerves or blood vessels, as in many other ichthyosaurians. In specimen 9913 an element possibly representing a lateral occipital rests upon the anterior side of the basioccipital. It has been split longitudinally and shows the passage of a large foramen. The complete outlines of the *supraoccipital* are not shown, but its upper portion is seen to extend forward a considerable distance to form part of the floor of a deep fossa between the posterior arms of the parietals.

The *opisthotic* and *stapes* are not certainly recognized on any of the several specimens that have been carefully examined, but there seems to be some reason for considering that the stapes at least was a less conspicuous element than in the later ichthyosaurs. The opisthotic may be represented by a somewhat indefinite element seen in specimen 9950. In the same specimen a slender rod of bone (*x*, pl. 5, fig. 1) extending from the otic region to the quadrate may represent the stapes. A careful examination of the well preserved quadrate has not shown the presence of a distinct pit for the accommodation of the distal end of a large stapes such as is present in some of the later ichthyosaurs.

The heavy *quadrate* of *Cymbospondylus petrinus* is closely and broadly united with the pterygoid, the squamosal, and the quadratojugal, so that the posterior angle of the skull must have been particularly rigid. The contact with the pterygoid extends inferiorly to the articular head of the quadrate and reaches up to the middle height of the quadrate, where the pterygoid meets the squamosal. The median side of the quadrate which is in contact with the pterygoid extends forward as a broad plate much as in *Sphenodon*. On the outer side, the large quadrate foramen is overlapped externally in part by the supratemporal. The broad articular head of the quadrate is crossed transversely by a marked groove situated between an anterior and a posterior convex surface.

The general disposition of the typical palatine elements on the inferior side of the skull (pl. 4) is not materially different from that in *Ichthyosaurus*. In all cases the palate is largely roofed over, the median margins of the pterygoids approaching each other quite closely back to a point about opposite the middle of the orbits. The relation of the pterygoids to the palatines is similar to that in *Ichthyosaurus*. The posterior ends of the pterygoids are extended backward as prominent projections reaching a considerable distance behind the basioccipital. Between these processes and the wings of the pterygoids in contact with the quadrates there is a strongly marked groove on each side.

On both sides of the palate of specimen 9950 the posterior portion of what might be considered as the outer wing of the pterygoid is separated from the main body of the pterygoid by a distinct break having the same position in the two cases. If the separation indicated here is a natural parting of the bone, the posterior element evidently corresponds to the ectopterygoid.

The relations of the prevomers have not been clearly determined, but appear to be similar to those found in *Ichthyosaurus*. The hyoid elements are long, slender, slightly curved rods similar to the hyoids of *Ichthyosaurus* and *Baptanodon*.

In specimen 9913 an elongated element situated above the pterygoid may represent the epipterygoid.

The *lower jaw* is slender and elongated much as in the typical ichthyosaurs. The rami are united in the symphysis for about one-fourth the length of the jaw, and the anterior ends of the splenials are included in the symphysis. The much elongated dentary extends backward to a point almost even with the posterior border of the orbit. The narrowed anterior ends of the angular and surangular extend forward almost as far as the anterior end of the maxillary. In specimen 9950 the outer side of the splenial is exposed for a short distance below the middle of the dentigerous portion of the jaw.

On the outer side of the posterior portion of the mandible the angular and surangular occupy about the same relative areas as in *Ichthyosaurus*. No coronoid elevation is present, but the coronoid region of the surangular is broadened and flattened above, offering a considerable area for muscle attachment. In specimen 9950 there is on the inner side of the posterior end of the jaw either a coronoid reaching far back, or an element which has been known as the prearticular. In this form the splenial extends back to a point below the coronoid region, where it overlaps the inner plate of the angular. The splenial and the inner plate of the angular both overlap an element (see *Cn*, fig. 9, p. 236) which extends from the coronoid region almost to the posterior end of the jaw. It extends over the median side of the articular, and is distinctly separated from that bone. The relations of a similar element the writer has seen most clearly in an ichthyosaurian, no. $\frac{R}{1280}$, in the British Museum of Natural History. In this specimen the splenial extends back almost to the cotylus of the mandible, and partly covers the inner, upward-curving portion of the angular. Lying between the splenial and the surangular there is in the coronoid region a plate-like element occupying the position of the coronoid. This element extends backward from its normal position, passing between the inner plate of the angular and the inner side of the articular, and falling but a little short of reaching the extreme posterior end of the jaw. In a specimen of *Baptanodon* (no. 878) at the Carnegie Museum in Pittsburg the same relations of these elements have been noted, and the coronoid extends quite to the posterior end of the jaw.[52]

The articular of *Cymbospondylus petrinus* rises abruptly behind the cotylus where the thickened anterior end forms a heavy posterior buttress against which the quadrate articulates posteriorly. It extends backward to the posterior end of the jaw, where it is again considerably thickened. On all of the specimens that have been examined, the posterior portion is deeply excavated superiorly between the anterior and posterior thickened regions.

Dentition.—In general, the characters of the dentition of *Cymbospondylus* excepting the insertion are essentially similar to those of *Ichthyosaurus*. Both upper and lower jaws are set with conical teeth numbering from thirty to thirty-five for each ramus of the jaw. In some cases at least (figs. 10 to 12), the teeth are situated in completely enclosed bone pits. Though the anterior teeth seem to have somewhat more slender crowns than the most posterior ones there appears to be no close approach to the degree of differentiation seen in *Mixosaurus*. The amount of cement on the roots of the teeth seems to be small. The dentine is strongly folded toward the base. The enamel of the crown is finely but sharply striated.

MEASUREMENTS OF SKULL OF *C. petrinus*, No. 9950

Greatest length of skull on horizontal plane	1166 mm.
Length, anterior end of premaxillary to posterior border of pineal foramen	814
Length, anterior end of premaxillary to anterior border of left orbit	717
Length, anterior end of premaxillary to anterior end of maxillary	373
Greatest height of skull	365
Premaxillary, anteroposterior diameter	650
Anterior end of nasals to anterior border of pineal foramen	380
Supratemporal fenestra, anteroposterior diameter	190
Lateral temporal bar, anteroposterior diameter	160
Orbit, anteroposterior diameter	198
Orbit, height	115
Length of right ramus of mandible	1180
Mandible, height below middle of orbit	114

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[52] Gilmore, C. W., Mem. Carneg. Mus., vol. 2, pp. 97 and 98, and pl. 11, fig. 2.

Vertebral Column.—The most nearly complete specimen which has been examined (no. 9950) shows a practically complete vertebral series back to the middle caudal region (fig. 128). Excepting the dislocation of some of the anterior vertebrae, and a small gap above the pelvis, the series is unbroken. Out of the total number of 84 vertebrae present, 67 are evidently presacrals. The location of the sacral region is pretty definitely fixed, both by the position of the pelvis and by the reduction in length of the ribs. The elements of the pelvis are still in their natural positions with reference to each other, and the ilium on one side appears to have almost its normal relation to the vertebral column. Considering that these elements, as also the vertebral centra and arches, and the ribs, show little evidence of disturbance, it is fair to assume that the vertebra above the ilium was either next the point of attachment of the pubis or close to it. The ribs in this region are still of considerable length, and if the point of attachment is not located at this place it is probably somewhat farther back.

The number of presacral vertebrae present here exceeds considerably that of any other ichthyosaurian of which the writer has any information. In the typical *Ichthyosaurus* the number is ordinarily near 45. The extraordinarily large number of 54 presacrals is indicated recently by Broili[53] in *I. platydactylus*. In *Mixosaurus* the number seems to have been between 45 and 50. The number in *C. petrinus* is also larger than that in any other marine saurians excepting very long-necked forms, and suggests the possibility that the number of presacrals may have been reduced rather than increased in the later Ichthyosauria. A general reduction of the number in later forms might be correlated with the development of a highly specialized caudal fin, causing localization of the locomotor function in the distal caudal region, instead of distributing it through nearly the whole length of the tail.

In specimen 9950 there are eleven vertebrae in front of the anterior border of the coracoid and scapula. Although no definite determination of the posterior limit of the cervical region can be made, eleven vertebrae is a relatively large number for this portion of the column.

The atlas and axis are clearly shown in position in several speci-

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[53] Broili, F., Palaeontog., Bd. 54, Taf. 13.

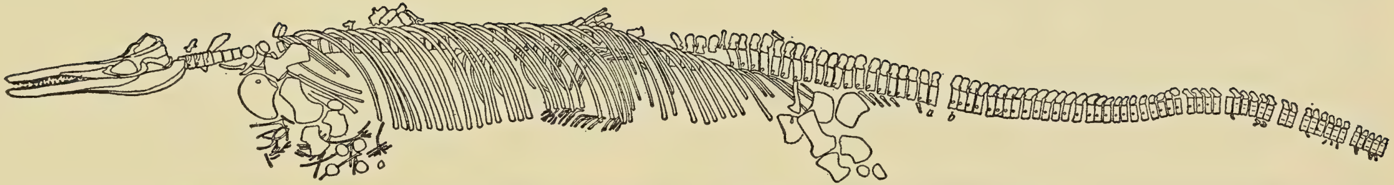


FIG. 128. *Cymbospondylus petrinus* Leidy. Outline of skeleton from specimen 9950, with caudal region and posterior limb added from specimen, 9947, × $\frac{1}{50}$; *a*, last caudal vertebra represented from the series of no. 9950; *b*, first vertebra represented from the series of no. 9947. The first vertebra represented in the series of no. 9947 seems to correspond in form and position of the diapophyses to a point somewhat farther back in the series than that represented by vertebra *a* of no. 9950.

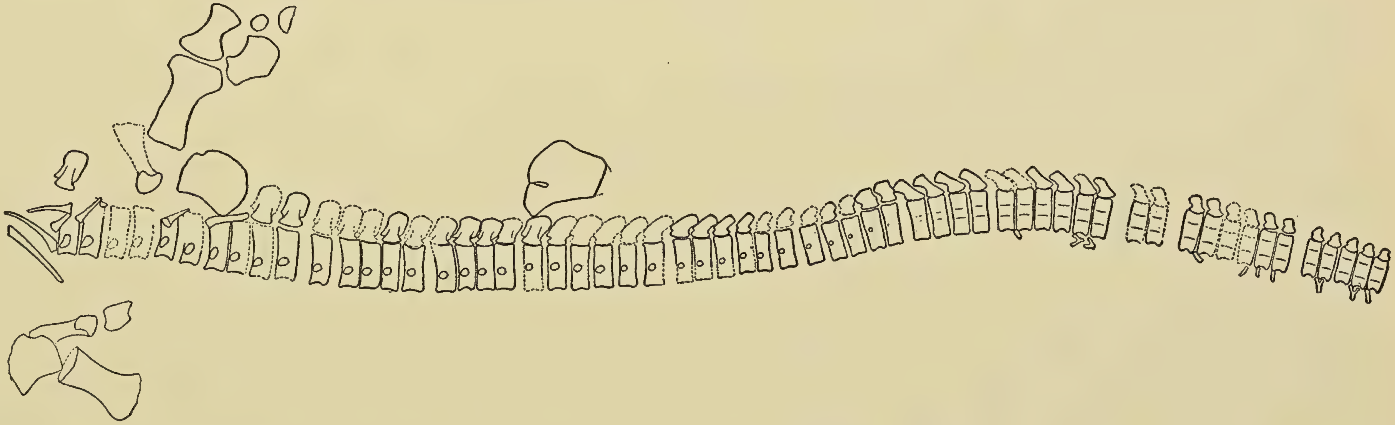


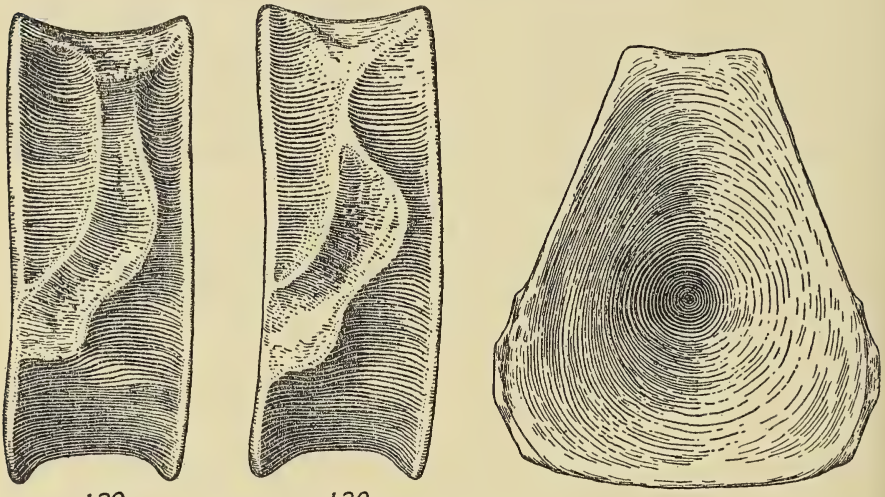
FIG. 132. *Cymbospondylus petrinus* Leidy. Caudal series with elements of the posterior arches and limbs, × $\frac{1}{20}$.

mens. (See pl. 8, also text-figure 58.) The centrum of the atlas is as wide, and in some cases almost as high, as that of the axis. Its anteroposterior diameter is considerably less than that of the axis. The anterior face is strongly convex, the convexity reducing the lateral and inferior borders to one-half or one-third the anteroposterior diameter of the centrum. The anterior face shows no depression into which the basioccipital might be received. The anterior face of the atlas is received in a deeply excavated articular face on the basioccipital. The posterior face of the atlantar centrum and the anterior face of the axis are both concave, and there is no suggestion of fusion of the two centra such as occurs in the later ichthyosaurs. The elements of the upper arch of the atlas as far as known are not materially different from those on the atlas of *Ichthyosaurus*.

The adjacent inferior borders of the atlas and axis may be obliquely truncated toward the plane of contact, for the intercalation of an intercentrum. There seems also to have been a small intercentrum between the third centrum and the axis, but none was present behind the third.

On the axis of no. 9950 there is a short diapophysis but no distinct parapophysis. In no. 9943 (fig. 58, p. 263) both diapophysis and parapophysis are present. On centra three and four of no. 9154 parapophyses of considerable size are present and small, nearly round articular facets are developed for the lower rib heads. On centrum six the parapophysis is very rudimentary, and on what appears to be the seventh it is absent. In no. 9950 the diapophysis on the fourth centrum is 43 mm. high, the parapophysis 17 mm. On the eighth centrum the corresponding dimensions are 45 mm. and 8 mm., and the parapophysis is generally much reduced. On the eleventh centrum there may be a minute rudiment of a parapophysis on the anterior margin. In specimen 9943 relatively large parapophyses are present back to the twelfth centrum (fig. 58, p. 263). On the thirteenth there is a trace of a parapophysis on one side only. In this specimen the parapophyses increase somewhat in size toward the dorsal region, and are larger both absolutely and relatively on the twelfth compared with the size of the diapophyses than they are on the fifth and sixth centra. The form and dimensions of the diapophyses remain about the same, back to the twelfth centrum. On the thirteenth they increase markedly in height, but the increase is not sufficient to make the height of the diapophysis on the thirteenth centrum equal the complete height of the diapophysis and parapophysis on the centra immediately preceding. The anterior cervical rib heads are divided proximally by a deep notch forming two distinct heads.

In those cervicals in which the ends of the centra are visible the degree of concavity is less than in the typical *Ichthyosaurus*. The excavation is comparatively slight until about half the distance to the center is reached where it runs in quite sharply.



129 130 131

Figs. 129–131. *Cymbospondylus petrinus* Leidy. Vertebrae from the middle and posterior dorsal regions, × ½.

Fig. 129, middle dorsal vertebra; fig. 130, posterior dorsal vertebra; fig. 131, posterior dorsal vertebra.

The vertical transverse cross-section of the cervical centra is much as in other ichthyosaurians, the transverse diameter being relatively large. In specimen 9943 the inferior side of the cervicals is distinctly carinate back to about the tenth vertebra.

In the dorsal region of specimen 9154, as also in 9950 (pl. 8), and others, the diapophyses are seen to elongate gradually as the centra come to be farther removed from the skull. In the middle dorsal region the lower portion of the diapophysis bends forward rather sharply from the nearly vertical upper portion. In the typical vertebrae of *Cymbospondylus petrinus*, the diapophyses differ from the ordinary form seen in *Shastasaurus* in that the anteroinferior border always seems to reach the anterior border of the centrum and be cut off by it (figs. 129 and 130); indicating that the lower portion of the rib head has come very near to intervertebral articulation, though there is no facet developed on the posterior border of the centrum in front.

At about the 36th to 38th centrum in no. 9950 the diapophyses move down the side of the centrum, and the articular faces are no longer confluent with the facets for the neural arches. The form of the centrum also changes from nearly circular in the anterior dorsal region to a high, narrow, triangular form in the posterior dorsal and anterior caudal region (pl. 9, and text-fig. 131). In this portion of the column the biconcavity of the centra is reduced to a very small area in the middle of each articular face, outside of which the surface is nearly plane.

In the middle caudal region the diapophyses are short and round, and have risen almost to the middle of the sides of the centra. The vertical transverse cross-section of the centra has also changed to a narrow hexagonal form.

The upper arches of the cervicals possess strong zygapophyses (pl. 8), on which the lateral faces are well separated and do not fall into the same plane, as occurs in *Ichthyosaurus*. In the dorsal region the zygapophyses are still well developed and the facets separate. In the caudal region the zygapophysial facets are much reduced, although the anterior and posterior projections of the upper arches are retained on most of the vertebrae.

The neural spines of the cervicals are somewhat compressed laterally, but are generally thicker than in *Ichthyosaurus*. In the dorsal region the spines are still considerably thickened. In no case, however, does the thickening of the spines approach that of *Shastasaurus altispinus*. In the caudal region of specimen 9950 the neural arches are considerably lower and thinner than in the dorsal region.

The form, and most of the important characters, of the caudal region are well shown in a large specimen of *C. petrinus* (no. 9947), in which there is present an excellent series of 59 vertebrae, aggregating twelve and one-half feet in length (fig. 132). The series begins near the pelvic region and extends back to within a few feet of the end of the tail. Immediately in front of this series of centra are broad-headed ribs with a length of 300 mm. or more, while the ribs with the centra opposite the pelvis are suddenly shortened to 120 mm. in length, and the rib heads are narrowed to a broad elliptical cross-section. The vertebrae immediately behind the pelvis of this specimen correspond in form, and particularly in form and size of the diapophyses and in their position on the side of the centrum, to a point in the column not farther forward than the seventy-first vertebra behind the head, or the sixth behind the pelvis, of the practically continuous series of specimen 9950. (See fig. 128.)

In the vertebrae immediately behind the pelvis the width of the centra transversely is somewhat less than the height, and the diapophyses are situated about one-third of the distance up the sides of the centra. The height of the neural arches is less than that of the centra, and the thin, broad spines are bent backward.

In passing backward through the caudal region from the pelvis to the thirtieth vertebra back of the femur, as here situated, the centra decrease very little in height but become much narrower transversely, and in the region of the thirtieth vertebra become relatively short inferiorly; the diapophyses rise to the middle of the centra, become reduced to small round knobs and disappear; the neural spines become shorter, are slightly wider distally, and begin to stand erect. The change from the recurved to erect position of the arches takes place at the thirtieth vertebra. The upper arch of the twenty-eighth vertebra turns backward as do those of all anterior to it, on the thirtieth the arch is erect and on the thirty-first it bends forward. Behind this point to the fifty-third vertebra the short upper arches all turn forward. The arches of the fifty-third and fifty-fourth, the last ones present in this specimen, are erect but not curved forward. In the region immediately behind the point where the upper arches begin to turn forward, the centra are slightly wedge-shaped, being shorter anteroposteriorly at the lower side. Though the diapophyses of the thirtieth vertebra are rather prominent no lateral apophyses are present behind this point. A short distance back of the bend the middle of the lateral face of each centrum bears two parallel anteroposterior ridges about twenty millimeters apart and separated by a shallow depression.

The changes in form of the caudal vertebrae which have been mentioned seem, as far as can be judged, to be connected with fairly definite changes in the curvature of the caudal region as shown in this specimen. As the series of vertebrae lies in the matrix the tail is bent slightly upward as far back as the thirtieth vertebra but from that point backward it is curved downward. At the point where the downward curvature begins the upper arches suddenly stand erect and then turn sharply forward, the diapophyses disappear, and the anteroposterior diameter of the inferior side of the centra becomes relatively short. The upward curvature of the tail as it lies in this specimen may be unnatural, and due simply to movement of the body after death. The downward curve of the distal region, being initiated as it is with noticeable modification in the form of the vertebrae, is evidently natural. Possibly the upward curve anterior to this is also natural, the distinct change in the vertebrae occurring at the crest of a long, upward curve as in *Mixosaurus*; or the distal region may have bent down from a nearly horizontal anterior region.

Facets for lower arches are present on the caudal centra in no. 9947, and the inferior side of the centrum is in all cases sharply angular, but chevrons have been seen only in the region back of the downward bend of the tail, where they are very small, though the facets for their reception seem to be larger than in the anterior portion of the tail.

The nature of the curvature in the caudal region of this specimen is in some respects not unlike that of *Ichthyosaurus*, as the upper arches are in relation to the centra but little larger than in that genus. The centra themselves are, however, much larger in the region of the bend, and beyond, than in any of the later ichthyosaurs, and the high thin centra doubtless served to broaden the fin somewhat as the high arches have done in *Mixosaurus*. The fact that the centra were higher suggests that less curvature of the distal caudal region was needed in order to widen the fin than was required in *Ichthyosaurus*, and that the bend was a gentle upward curve followed by a somewhat sharper downward flexure, as in *Mixosaurus*.

MEASUREMENTS OF THE SERIES OF CAUDAL VERTEBRAE IN SPECIMEN 9947

Approximate position of vertebrae, measured back from femur as situated in the matrix	Presence of diapophyses	Height of centrum	Anteroposterior diameter of centrum	Transverse diameter of centrum	Height and curvature of neural spine	Length of chevron
1	present	137mm.	51	112*a*		
12	present	128	49	115*a*	back slightly, 86	
27	present	114	48	80	back slightly, 61	
30	present	110	50 superior 44 inferior		erect, 57	
37	absent	114	48 superior 45 inferior	74.5	forward, 50	40*a*
41	absent	119	46	68	forward, 55	43*a*
48	absent	106	44	57*a*	forward, 43	40
53	absent	98	43	50*a*	vertical, 39	35

a, approximate.

Ribs.—Excepting on the anterior six to twelve vertebrae, the ribs of *C. petrinus* are all single headed (pl. 10). The short double-headed ribs have clearly notched heads, and articulate on distinctly separated diapophyses and parapophyses. As in *Shastasaurus*, in passing back through the vertebral series, the lateral apophyses of the vertebral centra remain widely separated to the point of disappearance of the parapophysis. If, as has been suggested by Yakowlew, the bicipital articulation was being developed in these forms through division of the rib head and of the vertebral apophysis with which it was in articulation, one would expect in passing forward to the region where separate apophyses actually exist to find the parapophyses gradually separating from the diapophyses. The fact that this is not the case may justly be urged against the view that the primitive ichthyosaurian possessed single-headed ribs. If a double articulation has been introduced in the American forms it must have appeared through the development of a parapophysis situated a considerable distance away from the diapophysis. If the double articulation extended from the cervical region out to the dorsals, the progress was most probably through the formation along the line of advance of rudimentary apophyses with no function of articulation. As yet no reason has been given why independent processes should grow out from the region of the paropophysis and the lower head to meet and form an inferior articulation. In addition to the arguments that have been presented, it is to be remembered that some of the oldest known ichthyosaurian forms, *viz.*, members of the *M.* (*?*) *atavus* group, have distinct double articulations in the posterior dorsal region.

The ribs of the dorsal region of *Cymbospondylus petrinus* are rather heavy, but have in general the form seen in *Ichthyosaurus*. The heads are thick inferiorly, and the superior portion of the articular face curves away from the upper part of the diapophysis, evidently leaving a gap filled by cartilage as in *Shastasaurus*. The posterior dorsal ribs have remarkably wide heads, but nowhere has there been observed a tendency for the articulating surface to divide into two faces, as has been suggested in the case of *Mixosaurus*.

In specimen 9950 short caudal ribs are present with the anterior caudal vertebrae. As shown in plate 10, figure 7, they have nearly round articular heads, but are considerably broadened distally.

Abdominal ribs are found in considerable numbers with most of the larger specimens, but are usually too much scattered about to show definitely their relations to each other. With specimen 9154 there is preserved a considerable section of the abdominal plastron in which the elements have suffered no disturbance (pl. 10, fig. 8). As nearly as can be determined there are usually two transverse series of abdominal ribs for every pair of true ribs. Each transverse series consists of a V-shaped median piece and two lateral pieces. The median elements are heavy, and are only slightly flattened anteroposteriorly. They are not divided along the median line, as in some ichthyosaurs. The anterior end or the point of the V of each median piece extends forward on the median line as an overlapping knob-like process. Between the lateral ends of the median pieces are inserted the ends of the heavy discrete lateral pieces. The plastron presents as a whole an appearance of somewhat greater strength and robustness than that of the later ichthyosaurs.

Pectoral Arch.—The entire pectoral arch is well known excepting the interclavicle, which has never been recognized (pl. 11).

The *scapula* is not like that of any other ichthyosaur. The body of this element is strongly recurved so that the much expanded distal end is turned almost at a right angle to the proximal portion. The anterior part is also much broadened just in front of the proximal end. The form of this element is quite unlike that in any other Triassic genus. It approaches most closely the general form in *Ichthyosaurus*, particularly in the character of the anterior expansion, which occupies the position of the anterior hook in *Shastasaurus*. It differs from the type seen in *Ichthyosaurus* in its much greater proximal and distal expansion.

The form of the sickle-shaped *coracoid* does not correspond to that in any other ichthyosaurian genus. The nearest approach is found in *Delphinosaurus* of the Californian Upper Trias. In *Delphinosaurus* the position seems to be reversed anteroposteriorly, and the large perforation just anterior to the proximal articulation is absent. Perforations and emarginations in this region of the coracoid are ordinarily not remarkably persistent features. This character has however been recognized in all specimens of *C. petrinus* thus far examined, and together with other differences would seem to distinguish this form sufficiently.

The *clavicle* is uncommonly large and heavy. The middle portion is considerably expanded, but the ends are narrow. The median end seems to show a face of articulation for an interclavicle, but that element is unknown.

Pectoral Limb.—As yet we know certainly only the first three segments of the pectoral limb in *C. petrinus*, no specimen having been found in which the phalanges are in place or even certainly recognizable. Owing to early decomposition of the thinner portions of the paddles they have probably been scattered before the slow accumulation of calcareous mud could cover them. In all of the *Cymbospondylus* specimens that have been examined the limb elements are almost exactly similar to the limb of specimen 9154 previously described (Merriam, 1905, 2).

The humerus is in all cases a relatively slender element; though not greatly elongated, it is not greatly expanded distally. The radius is extraordinarily long and slender for an ichthyosaurian, and the median constriction is pronounced. Between the epipodial elements is a gap as wide as that in the limb of any typical shore reptile. The ulna is also relatively long and shows a median constriction. The posterior portion of this element begins, however, to show the expansion so frequently occurring in aquatic types, and the posterior notch has been almost closed.

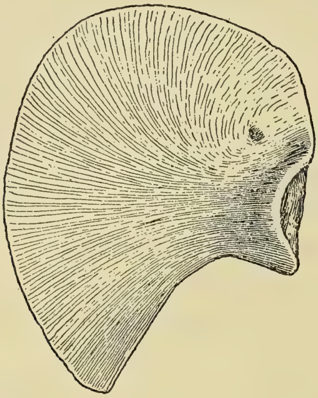


FIG. 133. *Cymbospondylus petrinus* Leidy. Coracoid showing anterior perforation, × $\frac{1}{6}$.

In specimen 9950 (pl. 11), as in several others, a transverse row of three small discoidal elements is seen next the distal end of the epipodial segment. These bones are almost circular in form, and they do not occupy the entire transverse space opposite the epipodials, so that they were evidently implanted in a heavy cartilaginous plate. In specimen 9148 a similar row of bones is seen. From their occurrence in this position there can be little doubt that these elements are carpals.

Pelvic Arch.—The elements of the pelvic arch (pl. 12, figs. 1–4) have been found in nearly their natural position in several specimens. The broad plate-like ventral elements were evidently united along the median line somewhat as in *Toretocnemus* (fig. 69, p. 55).

The *ischium* has much the same form as in *Delphinosaurus perrini* but may in some cases (pl. 12) show a shallow antero-internal notch giving it a form approaching that of the pubis of *Delphinosaurus.* Excepting the notch just mentioned the form is also not unlike that of the ischium in *Mixosaurus.*

The *pubis* resembles this element in *Toretocnemus* in that the proximal end is perforated by a large obturator foramen. In the only specimens which are perfectly preserved this opening is completely closed by bone. The transition from this form to that seen in *Shastasaurus* would be made easily by breaking down the bar of bone between the obturator foramen and the margin.

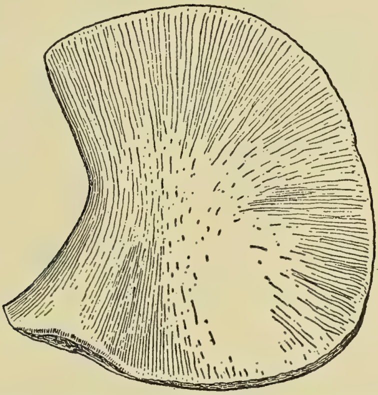


FIG. 134. *Cymbospondylus petrinus* Leidy. Ischium, specimen 9950, × ¼.

The *ilium* has a considerably expanded proximal head with an elongated and transversely expanded superior blade. The form resembles that of *Delphinosaurus,* though distinguished from it by the wider expansion of the blade and the absence of a posterior tubercle. Judging from its position in specimen 9950, the superior blade of the ilium was directed upward and forward to its sacral attachment.

Pelvic Limb.—The posterior limb is represented by the femur in the most nearly complete specimen, no. 9950. In specimen 9947 (pl. 12) a pelvic limb is present in which the femur has the same form and almost the same dimensions as in no. 9950.

The hind limb of no. 9947 shows the propodial and epipodial elements in their natural positions in the matrix, and with them are two small elements from the distal half of the paddle.

The *femur* is more slender than that of *Delphinosaurus*, *Toretocnemus*, or *Shastasaurus*. The nearest approximation to this type is found in *Mixosaurus*, but even here the distal expansion is relatively greater.

On the upper side of the femur the plane of the flattened distal end is continued over the proximal end with but little elevation. On the lower side of the proximal end a heavy trochanteric ridge is developed.

The distal end of the femur shows a broad terminal facet extending across nearly its whole width, and situated normal to the long axis of the bone. On this large facet the tibia articulates, standing in such a position that its long axis falls into a line almost coinciding with the long axis of the femur. Behind the broad terminal face of the femur there is a smaller facet standing almost normal to the plane of the terminal facet.

The *tibia* is longer than its greatest transverse diameter, and its proximal diameter is considerably greater than the distal. The median region is strongly constricted. The anterior side of the distal end is not expanded laterally beyond the limits of the median or shaft portion of the bone, but ends abruptly in a flat, roughened or pitted facet. Whether a small element has articulated on this face is as yet not certainly known.

The *fibula* articulates on the small posterior face of the femur, the situation of the bone being such that it is articulating largely against the posterior side of the femur with its narrower end. The median portion of the fibula is constricted. The distal end of the bone is greatly broadened compared with the transverse extent of the proximal and median portions, and shows a strongly curved terminal margin.

Of the other two elements present with the limb in specimen 9947, one is a small discoidal bone situated between the distal ends of the tibia and fibula, and presumably representing a mesopodial. The other bone is larger and is situated near the distal end of the fibula, but its form is too indefinite for determination.

The size and relative length of the epipodial elements of the posterior limb of specimen 9947 are much the same as in the elements of the corresponding region of the anterior limb of specimen 9950. Both epipodials show, however, a somewhat stronger median constriction than is seen in the anterior epipodials.

The most peculiar feature of the posterior limb is the situation of the tibia almost opposite the middle of the distal end of the femur, with the fibula located far back, and practically articulating on the posterior side of the femur.

Compared with the posterior limb of *Mixosaurus*, the available specimens representing the limb of *Cymbospondylus* may be considered, so far as known, to represent nearly the same stage of evolution as the hind limb of *Mixosaurus*.

MEASUREMENTS OF LIMB AND ARCH ELEMENTS, SPECIMEN 9950

Humerus.	
Greatest length	325 mm.
Greatest transverse diameter of distal end	200
Least transverse diameter of median region of shaft	133
Radius.	
Greatest length	200
Greatest transverse diameter of proximal end	143
Greatest transverse diameter of distal end	160
Least transverse diameter of median region of shaft	83
Ulna.	
Greatest length	185
Greatest transverse diameter of proximal end	121
Least transverse diameter of median region of shaft	95
Coracoid.	
Greatest anteroposterior diameter	312
Greatest transverse diameter	246
Scapula.	
Greatest anteroposterior diameter	357
Greatest width of distal end of posterior blade	195
Ilium.	
Greatest length	205
Ischium.	
Greatest anteroposterior diameter	200
Greatest transverse diameter	175
Pubis.	
Greatest transverse diameter, approximately	126

MEASUREMENTS OF POSTERIOR ARCH AND LIMB ELEMENTS OF SPECIMEN 9947

Femur.	
Greatest length	255 mm.
Transverse diameter of proximal end, parallel with flattened distal surface	117
Transverse diameter of distal end, parallel with flattened surface	170

Transverse diameter at narrowest portion of median region, parallel with flattened distal surface	83 mm.
Transverse diameter of tibial facet	152
Tibia.	
Greatest length	160
Transverse diameter of proximal end	143
Transverse diameter of median region	64
Transverse diameter of distal end	103
Fibula.	
Greatest length	157
Transverse diameter of proximal end	82
Transverse diameter of median region	78
Transverse diameter of distal end	132
Mesopodial (?).	
Anteroposterior diameter	46
Transverse diameter	42

Cymbospondylus piscosus Leidy

Cymbospondylus piscosus Leidy, Proc. Philad. Acad. Sc., 1868, vol. 20, p. 178.
Cymbospondylus piscosus (Merriam), Univ. Calif. Publ. Geol., vol. 3, p. 104.

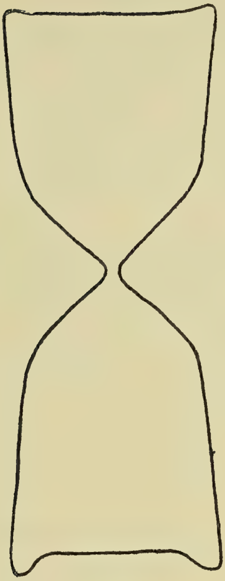
Anterior and posterior faces of dorsal vertebral centra deeply and regularly concave from the periphery to the center of the face. Length of dorsal vertebral centra equaling more than half of the height.

Known only from a single specimen found in the Middle Triassic near New Pass, about thirty miles west of Austin, Nevada.

This species is known only from a single specimen consisting of one nearly complete dorsal vertebra with parts of four others. No similar material has been observed in the collections from the West Humboldt Range, and a careful examination of the type locality has not resulted in the discovery of other specimens.

The characters of *C. piscosus* differ from those of *C. petrinus* and *C. nevadanus* sufficiently to warrant specific separation. As far as this form is known, there seems to be no reason for making a generic separation between it and the better known *C. petrinus*.

The vertebrae which are present in the type specimen (fig. 137) represent an individual smaller than the average of *C. petrinus* or of *C. nevadanus*. They belong in the anterior or middle dorsal region, as the parapophyses have disappeared and the diapophyses are elongated inferiorly. The upper arches are thicker than in *Ichthyosaurus*, and the zygapophyses are large.



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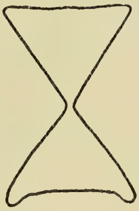

136

Fig. 135. *Cymbospondylus petrinus* Leidy. Anteroposterior section of a middle or anterior dorsal vertebra, × $\frac{3}{4}$.

Fig. 136. *Cymbospondylus piscosus* Leidy. Anteroposterior section of an anterior or middle dorsal vertebra, × $\frac{3}{4}$.

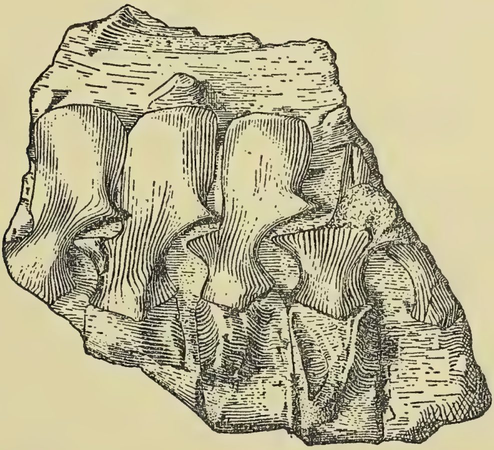

Fig. 137. *Cymbospondylus piscosus* Leidy. Lateral view of type specimen, × $\frac{1}{2}$.

Cymbospondylus nevadanus, n. sp.

Represented only by individuals of larger size than the average of known specimens of *C. petrinus*. Epipodials (?) of posterior limb much shorter and more massive than in *C. petrinus*. Tibia (?) very short and thick; distal end not narrower than proximal end, and without the flat anterior face present in *C. petrinus*. Middle caudal vertebrae high and narrow.

Type specimen, no. 10620, Univ. Calif. Col. Vert. Palae. (pl. 13), from New Pass, thirty miles west of Austin, Nevada.

In the summer of 1906 an expedition to New Pass, Nevada, visited the outcrops of Triassic limestone in that region, and made careful search for saurian remains in the hope of finding satisfactory material corresponding to Leidy's *Cymbospondylus piscosus*. Small limestone outcrops were found near the pass, and about three miles west of the New Pass mines. They are so distinctly set off from the areas of other rocks that there can be little doubt that the locality visited is the one from which Leidy's specimen of *Cymbospondylus piscosus* was obtained. Several isolated fragments of vertebrae and ribs were obtained; and one specimen (no. 10620) including a number of anterior caudal vertebrae, fragments of ribs, and several elements of the posterior limbs was found in place in the limestone. All of the saurian material from the New Pass limestones seemed to come from a single stratum about three feet in thickness. No new material was found which can be referred to *Cymbospondylus piscosus*. The Triassic limestones at the New Pass locality are stated by Professor James Perrin Smith to be of nearly the same age as the Middle Triassic horizon of the West Humboldt Range.[54]

The best specimen (no. 10620) consists of ribs, caudal vertebrae, and the epipodial limb elements, which were discovered in place in the limestone. Its characters differ from those of typical *C. piscosus* and *petrinus* of the type localities, and it appears to be necessary, for the present at least, to consider it as a distinct species. The lateral apophyses of the caudal vertebrae present are reduced to small rounded projections situated a short distance below the middle of the sides of the centrum. The vertebrae may be considered as representing the anterior or middle portion of the caudal region.

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[54] See list of species, p. 227.

The centra are considerably higher than wide and their anteroposterior diameter is relatively short. The anterior and posterior faces are so deeply concave that the central partition is almost if not quite broken through. The concave faces show a little peripheral flattening, but the sharpness of the concavity in the middle portion is not greatly in excess of that near the marginal area.

An upper arch associated with a centrum is considerably flattened laterally, though the summit of the blade is quite thick. The thickness is, however, nearly uniform for almost the whole of the anteroposterior diameter of the summit of the dorsal spine or blade. The summit is excavated or deeply pitted. The zygapophyses are much like those in the anterior portion of the caudal region of *C. petrinus.*

MEASUREMENTS OF A CAUDAL VERTEBRA, NO. 10620

Height of centrum	138 mm.
Transverse diameter of centrum	104
Anteroposterior diameter of centrum	53
Height of an upper arch	85
Anteroposterior diameter of an upper arch	52
Thickness of an upper arch at summit	18

Accompanying the vertebrae in specimen 10620 there are several ribs. They are round in cross-section near both the proximal and distal ends. The shaft increases in diameter very considerably at the rib head, but does not show much lateral compression. The articular face appears to be hollowed out to a considerable extent.

Associated with the ribs and vertebrae of no. 10620 there are two bones (pl. 13, figs. 4*a* and 4*b*) which do not correspond exactly in form to any elements that have been seen in other material thus far examined. They are elongated, with a long diameter a little less than the height of the vertebral centra. The middle portion is very slender, with a nearly round cross-section, and a diameter equaling about one-sixth of the length. Both ends are much expanded, one being nearly round and apparently deeply hollowed terminally. The other end is broadened and is considerably flattened in a plane standing almost at right angles to a less pronounced plane of compression of the opposite termination. These elements may represent caudal ribs from a region somewhat farther back in the series than the location of the more elongated and evenly rounded ribs described above. The less compressed end of the shorter bones corresponds quite closely with the proximal termination of the certainly known ribs described above, and is also somewhat smaller than the heads of these ribs. The flattened and expanded end may represent a modification in the terminal portion of a sacral rib, or may be the normal form in all anterior caudal ribs.

With the vertebrae and ribs of this specimen (10620) there are two elements, one of which (pl. 13, fig. 2) represents either a propodial or an anterior epipodial element of the posterior limb; the other (pl. 13, fig. 3) is either a posterior epipodial element of the hind limb or the ischial element of the pelvic arch. The first mentioned bone is much less elongated than either the femur or the tibia of *Cymbospondylus petrinus*, and is most nearly comparable with the tibia of *Shastasaurus* or *Delphinosaurus*. As there is no trace of a proximal trochanteric elevation, though the bone is perfectly preserved, it may, presumably, be considered as the preaxial epipodial element, but of a type quite different from that seen in *C. petrinus*.

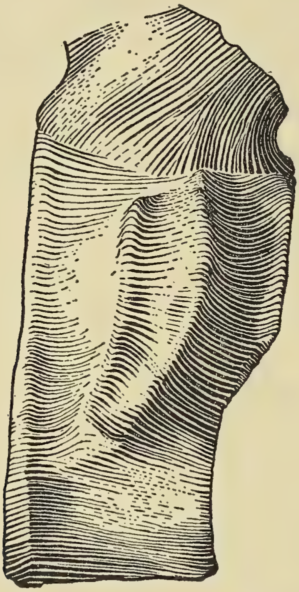


FIG. 138. *Cymbospondylus nevadanus*, n. sp. (?). Lateral view of anterior dorsal vertebra, × ½.

The other bone has almost the same axial diameter as the element referred to as the tibia, but is considerably thinner, particularly at the distal end. This element is slightly constricted medially, and greatly expanded distally. The distal expansion resembles the broadening of the distal end of the fibula in *C. petrinus*. If this element is the fibula, the limb must have been much broader than in *C. petrinus*, and the epipodial region relatively shorter. In any case the limb must have differed quite considerably from that of *C. petrinus*, and suggests a specialization of the epipodial region approaching that of *Shastasaurus*.

Another specimen (no. 10821) from New Pass, consisting of an isolated vertebral centrum (fig. 138) with a portion of the neural arch attached to it, represents the anterior or middle dorsal region. The centrum is relatively elongated compared with those of the same region in *Shastasaurus*, but does not differ greatly in this respect from the corresponding centra of *C. petrinus*. The anterior and posterior faces are deeply excavated. There is a single rib articulation which extends from the base of the upper arch to a point a little below the middle of the centrum, but the lower end does not swing forward to the anterior margin, as is generally the case in *C. petrinus*. This form can be only tentatively separated from *C. petrinus*, but with the differences shown in the small amount of material available it is not considered advisable to refer it to that species, and it may be referred to *C. nevadanus*.

MEASUREMENTS, NO. 10620

Posterior dorsal rib.	
Vertical diameter of rib head	60 mm.
Anteroposterior diameter of rib head	36
Caudal rib?	
Length	130
Greatest diameter of middle of shaft	21
Greatest diameter of less compressed end	48
Thickness of the less compressed end	35
Greatest diameter of more compressed end	53
Thickness of the more compressed end	25
Preaxial epipodial of posterior limb (?).	
Axial diameter	123
Transverse diameter of proximal end	140
Transverse diameter of median region	114
Transverse diameter of distal end	146.5
Greatest thickness of proximal end	65
Postaxial epipodial of posterior limb (?).	
Axial diameter	135
Transverse diameter of proximal end	95
Transverse diameter of median region	77
Transverse diameter of distal end	180
Greatest thickness at proximal end	50

MEASUREMENTS OF ANTERIOR DORSAL VERTEBRA, NO. 10821

Height of centrum	110 mm.
Transverse diameter of centrum	110
Anteroposterior diameter of centrum	64

Toretocnemus Merriam

Toretocnemus Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 251, pl. 24.

Vertebral centra relatively elongated. Neural arches not greatly thickened, but showing distinct lateral ridges. Caudal vertebrae with long Y-shaped lower arches. Middle dorsal rib heads sharply divided into lower head and tubercle. Diapophyses and parapophyses of vertebral centra widely separated in the middle dorsal region. Posterior limbs equaling the anterior in size. Limbs with three digits and a rudimentary fourth. Epipodial segments elongated and enclosing a wide space. Radius with median constriction, ulna notched only on the median border. Proximal row of mesopodial region including only three elements. Carpals and tarsals in linear series. Phalanges generally notched on one or both sides. Ischium and pubis plate-like; pubis very broad, and with obturator foramen. Ilium slender and elongated.

The type specimen, no. 8100, was obtained in the upper portion of the Trachyceras Beds at Bear Cove, on the east side of Brock Mountain, between Pit River and Squaw Creek, Shasta County, California. Other specimens evidently to be referred to this genus are known from the Trachyceras Beds.

Toretocnemus is distinguished from all of the other American Triassic ichthyosaurs by the double rib articulation of the middle dorsal region. (See fig. 59, p. 264.) In the characters of the limbs it has much in common with the genus *Merriamia*, excepting that the posterior limbs are relatively large. The pelvis is more primitive than that of any other Upper Triassic ichthyosaurian. (See fig. 69, p. 272.) It differs from the posterior arches of other Triassic forms, excepting *Cymbospondylus*, in the enclosing of the obturator foramen. The ilium seems to be more slender than in any other known form.

Toretocnemus californicus Merriam

Toretocnemus californicus Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 251, pl. 24.

The type specimen, no. 8100, Univ. Calif. Col. Vert. Palae., is the only determined material which has been completely exposed for study. A number of other small specimens from the same beds show similar characters. The type specimen was found embedded in a thin slab of shaly limestone which had been weathered in such a manner as to destroy a considerable part of the skeleton. The remaining fragments are not far removed from their natural positions. The parts present represent small fragments of the head, a vertebral series extending from the middle dorsal region to the middle of the tail, the pelvis nearly complete, the proximal half of both posterior limbs, a part of an anterior limb, and numerous ribs.

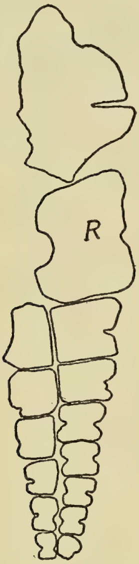


Fig. 139. *Toretocnemus californicus* Merriam. Anterior limb, natural size. *R*, radius.

This was the first American Triassic ichthyosaur in which the constricted phalangeal elements (fig. 139) were discovered. In the character of its limbs and pelvis this is the most primitive American Upper Triassic form. Whether the bicipital rib articulation of the middle dorsal region indicates primitive characters may perhaps be open to doubt. It is nevertheless most nearly paralleled by the structure of some of the earliest known European forms. The elongated vertebral centra are evidently of a more primitive form than the shorter centra of the shastasaurian type.

Merriamia Boulenger

Leptocheirus Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 251, May, 1903. Preoccupied by *Leptochirus.*

Merriamia Boulenger, Proc. Zool. Soc. Lond., vol. i, p. 425, Aug. 2, 1904.

Caudal vertebrae with elongated centra. Dorsal ribs single-headed. Coracoid elliptical, without pedunculation or emargination. Scapula with distal expansion and short anterior hook. Posterior limbs much smaller than anterior. Limbs with three digits and a much reduced rudiment of a fourth. Epipodial elements elongated and separated by a wide gap. Proximal row of mesopodial region with three elements, and intermedium supporting but a single element distally. Phalanges generally notched on one or both lateral margins. Angular element of mandible relatively small. Dentition undifferentiated, tooth crowns conical.

The genus is distinguished from *Toretocnemus* by the relatively small posterior limbs, and the single-headed rib articulation of the dorsal region. It differs from *Delphinosaurus* greatly in the form of the known elements of the limbs and of the pectoral arch. *Shastasaurus* represents a type of specialization somewhat similar to that of *Delphinosaurus* but much more extreme. *Mixosaurus* differs very considerably in the whole structure of the limbs, arches, and dentition.

This genus is represented by a single species occurring in the Trachyceras Beds of the Upper Triassic limestones of Shasta County, California.

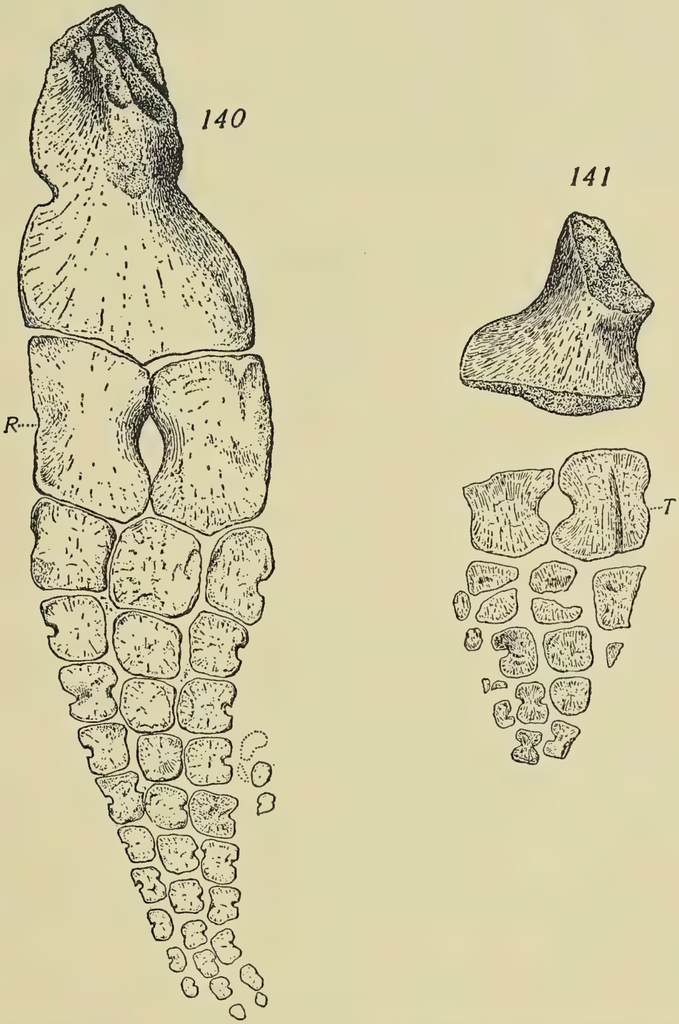
Merriamia zitteli (Merriam)

Leptocheirus zitteli Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 253, pls. 21, 22, and 23.

Merriamia zitteli (Boulenger), Proc. Zool. Soc. Lond., vol. i, p. 425, Aug. 2, 1904.

The type specimen, no. 8099, Univ. Calif. Col. Vert. Palae., was found in the Trachyceras Beds of the Hosselkus Limestone at Smith's Cove, between Squaw Creek and Pit River, Shasta County, California. It includes about one-half of the skull, the pectoral arch and limb, a large part of a pelvic limb, with a number of vertebrae, ribs, and abdominal ribs. In this form the tridactyl type of limb is better expressed than in any of the other Triassic forms known (figs. 140 and 141). A somewhat similar form of limb is seen in some of the longipinnate forms of *Ichthyosaurus*, as *I. acutirostris* Owen, *I. platyodon* Conybeare, and *I. tenuirostris* Conybeare.

With the pectoral arch of the type specimen of this species the clavicles were present in front of the coracoids. They are represented by two broad bars of bone meeting or possibly overlapping at the median line. The ends directed toward the scapulae are unfortunately broken away. The median ends are broad and are



Figs. 140 and 141. *Merriamia zitteli* (Merriam). Anterior and posterior limbs, × ½. Fig. 140, anterior limb; *R*, radius; fig. 141, posterior limb; *T*, tibia.

concave on what appears to be the posterior side. As far as can be determined these elements are much like the clavicles of *Shastasaurus*. An elongated triangular bone situated immediately behind the ends of the clavicles may represent the interclavicle. If this element is represented entire in this specimen, the posterior median arm or stem is very little developed, and is relatively smaller than in any other ichthyosaurian.

A caudal vertebra of this species (fig. 142) shows a considerably elongated form somewhat like that of *Toretocnemus*. The end faces are deeply concave and do not show a peripheral flattening of the face.

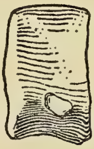


FIG. 142. *Merriamia zitteli* (Merriam). Lateral view of caudal vertebra, × $\frac{3}{4}$.

Delphinosaurus Merriam

Shastasaurus perrini Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 89, pls. 5, 6, and 7.

Delphinosaurus Merriam, Amer. Jour. Sc., vol. 19, p. 24, fig. 3, Jan., 1905.

Vertebral centra relatively much elongated, length of dorsal centra equaling one-half to three-fourths of their height. Neural arches of dorsal vertebrae much compressed laterally, though low lateral ridges or ribs are present. Scapula broad sickle-shaped, and without anterior notch or hook. Coracoid not pedunculate, with a well-marked anterior notch. Humerus narrower medially than in *Shastasaurus*. Epipodial elements of anterior limb both relatively elongated, and with median constriction. The genus ranges through the greater part of the lower or shaly horizon of the Hosselkus Limestone.

In the first study of *D. perrini*, the type species of this genus, the vertebrae were distinguished from those of the other forms referred to *Shastasaurus* by their extraordinary anteroposterior diameter. The typical species was, however, referred to the genus *Shastasaurus*, other distinguishing characters not being recognized owing to the fact that excepting ribs and vertebrae nearly all of the parts present in this species were lacking in the known species of *Shas-*

tasaurus. More recent discoveries have made known nearly the whole of the skeleton of this form excepting the distal portions of the paddles. While the skeletal structure obviously represents the shastasaurian group, it is distinguished from that of the typical species of *Shastasaurus* by several important characters other than those of the vertebrae. Only one species, *D. perrini*, is recognized.

Delphinosaurus perrini Merriam

Shastasaurus perrini Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 89.
Delphinosaurus perrini Merriam, Amer. Jour. Sc., vol. 19, p. 24, Jan., 1905.

Type specimen no. 9119, Univ. Calif. Col. Vert. Palae. Since the discovery and description of the type material three valuable specimens representing this species have been obtained. A considerable number of more fragmentary specimens indicate the geologic range of the species.

No. 10998 (pl. 7, fig. 3), a small specimen about two metres long, represents a large part of the skeleton, extending from the anterior region of the skull to the end of the tail. This specimen is somewhat smaller than the type of *D. perrini*, and the vertebral centra are slightly less elongated in proportion to their height, but the resemblance to that species is in general very close. In this specimen the vertebral column includes 115 centra and appears to be nearly complete. About 75 of the centra are in the caudal region, which constitutes nearly one-half of the length of the column. The remaining 40 vertebral centra reach to the posterior part of the skull. Beneath the skull, weathering and imperfect preservation of the bones make it difficult to determine how many centra have been present, but there could hardly have been more than ten, and the number was probably somewhat less. The total number of vertebrae for the presacral region including an estimate of between five and ten for centra possibly lost beneath the skull would be near 45, or about the same as in *Ichthyosaurus*. In the type specimen there are 35 presacrals present, and the estimated number for the whole presacral region is also about 45.

The caudal region of no. 10998 terminates with a series of very small centra about ten millimeters in height. It appears to be nearly complete, though a few more terminal centra may have been present originally. In the distal half of the caudal region, following a slight downward curvature, the tail is bent upward and down again as in *Mixosaurus*, and at the extreme distal portion it is curved upward again. As the whole vertebral column is turned partly over, and is somewhat disturbed in this specimen, it may perhaps be questioned whether the curvature seen here represents the normal position of the vertebral column in the caudal fin. There is, however, relatively less disarrangement of the vertebral centra in the caudal region than elsewhere, and a part of the sinuosity shown may represent a normal vertical curvature, somewhat resembling that of *Mixosaurus*.

In the vertebral column of the type specimen of *D. perrini* there are between 25 and 30 vertebrae in that portion of the caudal region anterior to the bend of the tail. In specimen 10998 the beginning curvature seems to occur between the 25th and 35th caudals.

Throughout the whole vertebral column the centra are extraordinarily long for ichthyosaurians. In a middle dorsal of the type specimen the ratio of height to length is 1:84, and in an interior caudal 1:56.

The spines of the upper arches are not greatly elongated in any part of the column, but are in general considerably compressed laterally (see fig. 32*a* and 32*b*, p. 245), particularly in the dorsal and anterior caudal regions. The strong lateral compression of these arches stands in decided contrast to the wide cross-section of the neural spines of the dorsal region in some forms of *Shastasaurus*. That the flattened form of spine is derived from an originally thicker type is suggested by the distinct lateral rib situated about the middle of the expanded blade of each arch.

The *rib* articulation is evidently similar to that of *Shastasaurus*. Though little is known of the most anterior cervical vertebrae, they seem to have supported bicipital ribs. From the anterior dorsals back to the caudals the ribs were single-headed. In the posterior dorsal and anterior caudal regions the rib heads are well preserved, and there is no evidence of bifurcation of the heads, as has been suggested for *Mixosaurus*.

In the anterior dorsal region the rib heads articulate mainly upon the large diapophyses, but the upper portion seems to have been distinctly in contact with the base of the neural arch. (See fig. 26, p. 243.) About as far back as the twenty-fifth vertebra the bases of the upper arches are produced laterally over the tops of the centra so that the lateral extremities are immediately over the lateral faces of the diapophyses. The ends of these lateral spines of the neural arches appear distinctly truncated, and the lateral faces were evidently continuous with the articulating faces of the diapophyses.

The rib articulation remains high up on the side of the centrum as far back as the middle of the dorsal region, where it suddenly drops to the middle of the centrum.

In all specimens examined the lower arches of the caudals in this species are very long, while the right and left elements are fused inferiorly to form a spine which may be considerably longer than the V-shaped portion above. The articulation of the lower arches is intervertebral, and pairs of distinct facets are formed on the adjoining margins of the centra with which the arches are in contact.

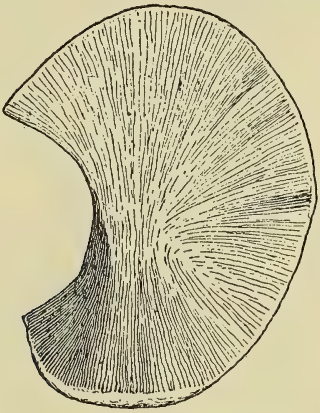


FIG. 143. *Delphinosaurus perrini* Merriam. Scapula, × $\frac{3}{4}$.

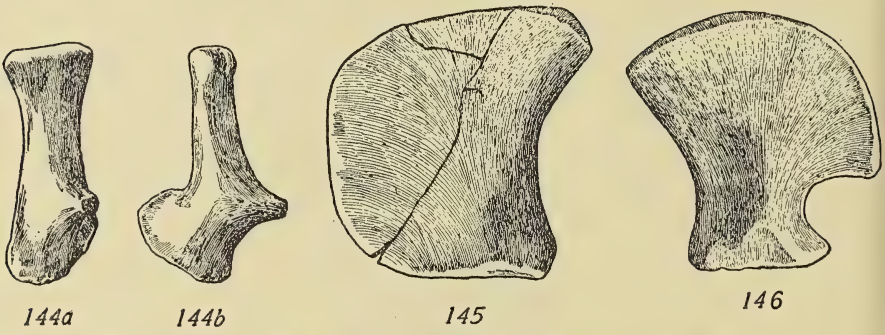
The long dorsal ribs of *D. perrini* are of the same general form as those in *Shastasaurus*, but do not show as pronounced outward curvature of the upper portion of the articular face as in *Shastasaurus altispinus*. In the dorsal region the rib shaft is furrowed anteriorly and posteriorly for a large part of its length.

The *pectoral arch* was represented in the type specimen by a fragment of a coracoid. In specimen 9082 (pl. 14) the scapula, coracoid and probably the clavicle are preserved. The scapula (fig. 143) differs from that of all other ichthyosaurians in having a broadly sickle-shaped or lunate form without an anterior hook as in most other Triassic forms. The posterior margin is much shorter than the anterior and is strongly concave. It is separated from the proximal and distal margins by sharp angles. The anterior margin is regularly convex, and curves into the proximal and distal margins, from which it is not distinctly separated.

The coracoid has the form of an ellipse with a strong emargination at one end. The general outline is somewhat similar to that of *Ichthyosaurus ingens* Theodori.

Large curved elements which may represent the clavicles are present on the slab in specimen 9082, and are in contact with the scapula. No interclavicle is known.

With specimen 9082 both *anterior limbs* are present with the pectoral girdle (pl. 14), but in both limbs the phalangeal elements have been lost or scattered. The propodial and epipodial segments are different from those of any other known form. The humerus is considerably narrower medially than in *Shastasaurus*, and is much more abbreviated and of very different form from that in *Merriamia* or in *Cymbospondylus*. Excepting *Cymbospondylus*, this is the only known Triassic type in which both epipodials of the anterior limb show a median constriction. The ulna and radius have nearly the same form. In both bones the median border is concave, and the lateral border is deeply notched. Both elements are relatively much longer than in *Shastasaurus*, and approach the length of the humerus.



FIGS. 144*a*–146. *Delphinosaurus perrini* Merriam. Elements of pelvis, $\times \frac{9}{20}$.

FIG. 144*a*, ilium, posterior view; fig. 144*b*, ilium, median side; fig. 145, ischium; fig. 146, pubis.

A proximal and a distal row of carpals, including three elements in each row, are present. The proximal row is evidently complete, the same elements appearing in both right and left limbs. The distal row may have included more elements, though they are not represented in this specimen. In the first row the radiale shows an anterior marginal notch as in the longipinnate ichthyosaurs. The intermedium is large and subquadrate in form in both right and left limbs. The ulnare is relatively small and nearly circular in both limbs. In the second row of carpals the third element from the anterior border is almost immediately opposite the ulnare, and shows the same dimensional relations to carpalia one and two that the ulnare shows in relation to the radiale and intermedium. The noticeable reduction of the posterior elements in both rows of the carpus seems to indicate a reduction of the posterior digits equaling or exceeding that in the tridigital manus of the genus *Merriamia.*

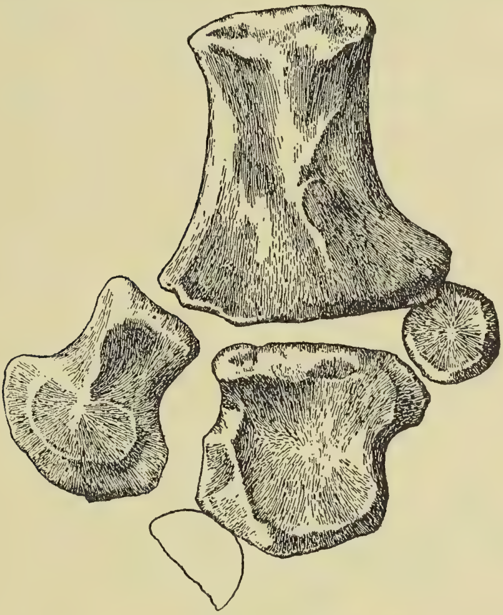


Fig. 147. *Delphinosaurus perrini* Merriam. Posterior limb, × $\frac{3}{4}$.

The rounding of the margins of the carpal elements evidently indicates the presence of considerable cartilage, and suggests a fairly high stage of specialization.

The elements of the *pelvis* are all shown in the type specimen (pl. 17, and text-figs. 144 to 146). An ischium and a pubis of similar character are also present in specimen number 9086. The determination of these bones was to some extent tentative in the study of the first specimen, but seems now fully justified by what is known of the pelvis of other Triassic ichthyosaurians in which the position of the elements is definitely determined. The pelvic bones are in general much like those of *Shastasaurus*. The ilium is distinguished from that of all the other Triassic genera by the presence of a tubercle near the outer side of the proximal end. This tuberosity is indicated on both of the known specimens, and has not thus far been seen in any other form. The ischium is somewhat broader than in *Shastasaurus*. In the pubis the proximal end is not as wide as in *S. pacificus*, while the distal hook is not as strongly curved as in that form.

The *posterior limb* (fig. 147) shows much the same stage of development as the posterior one in *S. osmonti* (no. 9608; see figs. 100–101, p. 284). The femur is more distinctly abbreviated than in *Cymbospondylus*, and is somewhat broader than in *S. osmonti* (no. 9608). The tibia and fibula both show a median constriction. The tibia is much larger than the fibula and has nearly the same width at the two ends. The fibula is expanded at the distal end, but as in *Cymbospondylus* the proximal end is barely wider than the middle of the shaft. Several discoidal limb elements are present with the hind limb of the type specimen, but it is uncertain whether they represent mesopodial or phalangeal elements.

A considerable part of the *skull* is present with specimen 10998, and a portion of the cranium with specimen 9082, but as yet it has not been possible satisfactorily to free the delicate bones from the hard matrix.

Of specimen 9082 there are given below the measurements of three anterior dorsal vertebrae, which correspond in their position to about the 15th, 16th, and 17th in the vertebral column; a fourth is near the position of the 25th vertebra.

MEASUREMENTS, SPECIMEN 9082

15th vertebra, anteroposterior diameter of centrum	21.3 mm.
15th vertebra, height of centrum	30
15th vertebra, height of upper arch	41
16th vertebra, anteroposterior diameter of centrum	21.5
16th vertebra, height of centrum	30
16th vertebra, width of centrum	33.5
17th vertebra, anteroposterior diameter of centrum	21.5
17th vertebra, width of centrum	33.5
25th vertebra, anteroposterior diameter of centrum	24
25th vertebra, height of centrum	30
25th vertebra, width of centrum	45
25th vertebra, height of upper arch	41

MEASUREMENTS, SPECIMEN 9086

Anterior caudal vertebra, anteroposterior diameter of centrum	28 mm.
Anterior caudal vertebra, transverse diameter of centrum	*a* 48
Anterior caudal vertebra, height of centrum	52
Anterior caudal vertebra, height of upper arch	48
Anterior caudal vertebra, length of chevron	72
Anterior caudal vertebra, length of stem of chevron	39
Ilium, greatest length	55
Ischium, greatest length	61
Ischium, greatest width	56

a Approximate.

VERTEBRAE OF SPECIMEN 10998

Number of vertebra counted from anterior end of column*	Height of centrum	Transverse diameter of centrum	Anteroposterior diameter of centrum
3	27 mm.		
9			18
20			22
23	35		
36	36		
38		21	
48	33		16
65	23		9
70			9
84	19		
105	16		4.5
110	*a*12		4.5

* To the number of vertebrae behind the skull about 5 to 10 vertebrae should be added to compensate for a number which have been lost from the anterior end of the column.

Shastasaurus Merriam

Shastasaurus Merriam, Amer. Jour. Sc. 1895, vol. 4, p. 56.
Shastasaurus (Dames), Sitzb. d. Acad. d. Wiss. Berlin, 1895, p. 1048.
Schastasaurus (Boulenger), Zool. Record. Rept. p. 29, 1896.
Shastasaurus (Yakowlew), Verh. d. Kais. Russ. Min. Ges. Bd. 40, p. 194.

Vertebral centra relatively short, neural spines often greatly thickened. Bicipital ribs only in anterior part of series. Coracoid pedunculate; scapula expanded distally, and with anterior hook. Pubis and ischium much expanded distally, pubis with deep obturator notch. Propodials and epipodials of anterior limb relatively much shortened. Epipodial elements separated by a cleft excepting in extreme cases of shortening (*S. careyi*). Posterior elements of epipodial and mesopodial series relatively reduced.

Typical species, *S. pacificus*, from the upper portion of the Trachyceras Beds of the Hosselkus Limestone of Shasta County, California.

This genus is characterized by the extreme specialization of the limbs and of the neural vertebral arches. Both propodial and epipodials of the anterior limb are greatly shortened, the most extreme form appearing in *S. careyi*, where the length may not amount to more than 75 per cent. of the width. With the reduction in length of these elements there has occurred also a reduction of the posterior elements of the limb, so that the posterior epipodial and probably the third or posterior mesopodial were much smaller than in the other genera. Judging from what is known of this reduction, the posterior digit has also suffered reduction, and the limb may have been reduced nearly to a two-fingered type. The elements of the arches are generally thick and heavy. Particularly is this true in the case of the coracoid, which is also exceptionally narrow anteroposteriorly near the proximal end.

The skull is fairly well known in this genus, but has not shown any very marked characteristics.

The species occur in the Hosselkus Limestone of Shasta County, California, ranging from the lower part of the Trachyceras Beds to the massive upper limestones. *S. osmonti* seems to range from the Trachyceras Beds, where it is common, to the upper, massive limestone, where it is rare. *S. alexandrae*, *S. altispinus*, and *S. pacificus* are known from the upper portion of the Trachyceras Beds. In the upper, massive limestones *S. careyi* is the common form, vertebrae of *S. osmonti* being seen with it occasionally. *S. careyi* may possibly occur also in the upper part of the lower horizon.

The history of the genus seems to show pretty clearly a gradual evolution out of an earlier, smaller, and less specialized type like *S. osmonti*, to the much larger and more highly specialized *S. careyi*, which is almost the only form seen in the upper, massive limestones.

As yet no true *Shastasaurus* is known from the Middle Triassic formation of Nevada.

From the evidence of a very small quantity of fragmentary material it appears possible that ichthyosaurian forms at least allied to *Shastasaurus* have had a wide geographic distribution in Triassic times. From an examination of the measurements of Hulke's *Ichthyosaurus polaris* the writer has suggested (1902, 2, p. 88) that this form closely resembles in character the posterior dorsals of *Shastasaurus*. More recently Yakowlew (1902, 1, p. 194) has described additional material from this region. This he refers to the species *polaris*, which is considered by him to be a true *Shastasaurus*. As is indicated elsewhere (p. 385) this form is possibly nearer to *Cymbospondylus* than to *Shastasaurus*.

Shastasaurus osmonti Merriam

Shastasaurus osmonti Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 93, pls. 8, 9, 10, and 11.

Vertebral centra relatively longer than in *S. careyi*, and somewhat shorter than in *S. pacificus* or *altispinus*. Neural arches of dorsal vertebrae showing more lateral compression than *S. careyi* and *altispinus*. Coracoids and humerus much broader and thicker than in *S. alexandrae*. Humerus less abbreviated than in *S. careyi*.

This species was the first American Triassic ichthyosaur of which enough material was found to make possible a satisfactory determination of its systematic position. The type specimen consisting of thirty-five vertebrae from the anterior portion of the column, together with the most important elements of the anterior arch and limb, was obtained by Mr. V. C. Osmont from the Atractites Beds of the Hosselkus Limestone, at Smith's Cove, on the west side of Brock Mountain, between Squaw Creek and Pit River, in Shasta County, California. Several other specimens representing about as large a portion of the skeleton as the type, also many isolated bones or small parts of skeletons, have been obtained. The species ranges from well down in the Trachyceras Beds of the lower or more shaly division of the Hosselkus Limestone up into the higher, massive, gray limestone horizon represented in part by the Spiriferina Beds. It is most common in the upper part of the lower or more shaly division.

The species includes individuals probably ranging from 12 to 18 or 20 feet in length.

In the type specimen, no. 9076, Univ. Calif. Col. Vert. Palae., a series of vertebrae shows the characters of the centra from the axis to the 36th centrum. (See fig. 57, p. 263.) As far back as this series of centra extends, the faces of articulation of the diapophyses are confluent above with the articular faces for the neural arches. In the anterior region of the column the diapophyses are relatively short, and well developed parapophyses are present below them. In proceeding backward in the series the diapophyses gradually elongate, and in the middle dorsal region develop a knee-like bend at about the middle of their height, the lower portion of the apophysis swinging forward almost to the anterior margin of the centrum. Behind the anterior ten or eleven vertebrae the parapophyses are reduced and were not functional. The last minute trace appears on one side of the eighteenth centrum.

The upper arches of the vertebrae in the most anterior cervical region possess slender spines with a round cross-section. The spines of the dorsal arches are thick compared with those of *Ichthyosaurus*, but they are more compressed laterally than in *S. altispinus* or *S. careyi.*

The ribs are rather heavy and tend to develop the outward curvature of the upper portion of the articular face, permitting a rocking movement, but much less strongly than in *S. altispinus* (see figs. 66*a* and 66*b*, p. 269) or *S. careyi.*

In specimen 9081 there is present the posterior portion of a cranium of *S. osmonti* with the cervical and anterior dorsal vertebrae, the pectoral girdle, and portions of both anterior limbs. The limb and arch elements are slightly smaller than those of the type specimen, but the general form and proportions are the same. In this specimen the series of cervical vertebrae seems to be complete, though the anterior individuals are displaced somewhat. Immediately behind the articular face of the basioccipital is a small, thin centrum representing the atlas. One surface shows a funnel-like concavity which extends inward almost from the margin. The opposite side is gently convex, excepting a small, shallow, central concavity covering not more than one-third of the area. The widely concave side apparently represents the posterior face, the anterior face of the centrum considered as the axis being also deeply concave. Its funnel-shaped form is, moreover, not the form of excavation that would probably develop in articulation with the basioccipital. The posterior articular face of the basioccipital is strongly convex, and the middle of the face evidently rested in the small concave middle area of the anterior side of the atlas.

The atlantar centrum differs from that of *Cymbospondylus* in the development of the slight concavity on the otherwise convex anterior face, and in the apparent absence of distinctly marked lateral faces. The addition of a certainly known atlas to the vertebral series of *Shastasaurus* suggests that, as indicated in the original description, the number of cervicals with attached intercentra may be larger than in *Ichthyosaurus*.

A valuable specimen (no. 9608; pl. 17, fig. 1) found during the season of 1903 appears to correspond to *S. osmonti*, and shows the previously unknown vertebrae and ribs of the posterior dorsal, sacral, and anterior caudal regions, together with all of the pelvic elements, and the first two segments of the posterior limb.

Over thirty vertebrae are present with this specimen, the number being about evenly divided between presacrals and postsacrals. They have been but little disturbed, but are so turned that measurements of their height cannot be made in most cases without destroying neural arches or ribs. The length and height of a dorsal about fifteen vertebrae in front of the pelvis are nearly the same as in the type specimen of *S. osmonti*. The anterior caudals are much shorter than the corresponding centra of *D. perrini*. A comparison of the vertebrae of this form with *S. pacificus* is difficult, as the portion of the vertebral column represented in that species is here covered by the ribs. The neural spines of the most posterior dorsals are, however, much like those in the type specimen of *S. pacificus*. The pelvis so far as known is quite different from that of *S. pacificus*.

Short caudal ribs and long-spined Y-shaped chevrons are present on the anterior caudal vertebrae.

MEASUREMENTS OF VERTEBRAE, SPECIMEN 9608

Anteroposterior diameter of the centrum of a posterior dorsal about fifteen vertebrae in front of the pelvis	32 mm.
Height of 15th centrum in front of pelvis	69
Height of a neural arch about seven vertebrae in front of the pelvis	66
Anteroposterior diameter of an anterior caudal centrum immediately behind the pelvis	32
Height of neural arch of anterior caudal immediately behind the pelvis	52
Length of an anterior caudal chevron	*a* 114

a Approximate.

The coracoid of the type specimen of *S. osmonti* is characterized by its thickness, and the extreme narrowness of the proximal portion. The form of the scapula is much like that in some mosasaurian genera. The greatly abbreviated and thickened elements of the anterior limb, though shorter and thinner than in *S. alexandrae*, are easily distinguished from the corresponding elements of *S. careyi*, which are much more specialized in these particulars.

Near the humerus in specimen 9081 is a row of three paddle bones from the mesopodial or phalangeal region (pl. 15, fig. 4). Two of them are of nearly equal size, and the third element, at one end of the row, is much smaller. As has been stated elsewhere (p. 292) there is reason to suppose that the relatively large size of the anterior elements of the limb was accompanied by reduction of the posterior elements to such an extent that the limb came to have only three digits, the most posterior of which was relatively small.

Other discoidal paddle bones are present with specimen 9081, and in one of these the margin is distinctly pitted and grooved (pl. 15, fig. 3).

The pelvic elements seen in specimen 9608 (pl. 16) are much like those of *Delphinosaurus perrini*, though the pectoral arch is very different. The ilium is more robust than in *Toretocnemus*. The proximal end is broadened transversely much as in *Delphinosaurus* and *Cymbospondylus*. There is no evidence indicating the presence of a posterior tubercle such as seems to be present on the ilium of *Delphinosaurus*.

The ischium is a broad, plate-like element, but is not as wide as in *Delphinosaurus* or in *Cymbospondylus petrinus*.

The pubis is intermediate in form between that of the *S. pacificus* and the corresponding element of *D. perrini*. It differs from the pubis of *S. pacificus* in the form of the posterior portion of the proximal end, which in *S. pacificus* curves inward and forward toward the posterior hook of the expanded distal portion. In the type specimen of *S. pacificus* the proximal end is broader and the posterior proximal hook more pronounced than in specimen 9608.

Of the left hind limb (pl. 16, fig. 6) the elements belonging to the propodial and epipodial segments are but little disturbed. The femur is a short robust bone with a well developed trochanteric ridge, and a somewhat expanded distal end. It is a little more slender than in *D. perrini*, but is not more elongated than in *Ichthyosaurus*. It is relatively heavier and broader than in *Cymbospondylus*.

Each of the epipodial elements shows a median constriction, and they are in consequence of this separated by a wide gap. The tibia is much larger than the fibula, and is almost equally expanded at the two ends. The fibula is much expanded distally, while the proximal end is hardly broader than the median portion of the shaft. The characters of the epipodial elements are in general much like those of *Delphinosaurus perrini* excepting that both elements are a little more slender than in that form. With the determinable limb bones of this species are several discoidal limb elements which may represent tarsals or possibly phalanges. In one of these rounded elements the thickness of one side is much greater than the other, probably indicating its position near the border of the limb, and the peripheral surface is distinctly concave.

MEASUREMENTS OF SPECIMEN 9608

Pelvic Elements.	
Ilium, length	110 mm.
Ilium, transverse diameter of distal end	60
Ischium, length	109
Ischium, greatest width	85
Pubis, length	120
Pubis, greatest width of distal blade	105
Pubis, width of proximal end	67
Posterior Limb.	
Femur, length	132
Femur, width of proximal end	78
Femur, greatest diameter of proximal end	84
Femur, width of distal end	117
Tibia, length	96
Tibia, width of proximal end	92
Tibia, width of narrowest portion of shaft	66
Tibia, width of distal end	108
Fibula, length	94
Fibula, width of proximal end	41
Fibula, width of distal end	86

Of the skull only the most posterior portion of the cranium and of the lower jaw are present in specimen 9081. In the posterior parietal region the relations of the parietals are seen for the first time in *Shastasaurus*, the posterior arms of the parietals extending backward behind the parietal arch of the squamosal, as in *Cymbospondylus* and *Baptanodon*.

The relations of the temporal, supratemporal, postorbital and quadrate are distinctly shown, and are much as in *S. alexandrae*. The articular face of the quadrate shows a weak transverse groove.

The form of the basioccipital appears to be different from that in *Ichthyosaurus* or *Baptanodon*. The inferior side of this element is produced as two prominent hypapophyses not unlike the corresponding prominences in *Cymbospondylus* or in the Mosasauria. The posterior articular face is strongly convex.

Shastasaurus alexandrae Merriam

Shastasaurus alexandrae Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 96, pls. 12 and 13.

Vertebral centra much as in *S. osmonti*, but much longer anteroposteriorly than in *S. careyi*. Anterior cervical ribs double-headed; posterior cervical or anterior dorsal ribs single-headed. Elements of the pectoral arch and anterior limb much broader and thinner, and anterior notch of the humerus much wider than in *S. osmonti*.

Type specimen, no. 9017, Univ. Calif. Col. Vert. Palae., from the upper part of the Trachyceras Beds of the Hosselkus Limestone, one-quarter of a mile south of Smith's Cove, Brock Mountain, between Squaw Creek and Pit River, Shasta County, California. Fragmentary material apparently belonging to this species has been found at other localities in this region.

The type specimen of this species represents an individual of nearly the same size as the type of *S. osmonti*, but the cervical and anterior dorsal vertebral centra are relatively a little longer than in that species. The coracoid, scapula and humerus are all much broader and thinner than the corresponding bones in *S. osmonti*. Though the two species are closely related, the differences are of sufficient magnitude to deserve recognition in an attempt to express in a classification the amount of variation in this genus.

The type specimen is the only individual of a typical *Shastasaurus* of which any considerable portion of the skull is known. Most of the elements are shown in this specimen excepting the rostral region. The cervical vertebral series is complete, and the elements which are of importance in determining the nature of the change in the rib articulation from double to single have been almost perfectly preserved.

Shastasaurus pacificus Merriam

Shastasaurus pacificus Merriam, Amer. Jour. Sci., 1895, vol. 4, p. 56, figs. 1 and 2. Univ. Calif. Publ. Geol., vol. 3, p. 102, pl. 14, figs. 1 and 2, text-fig. 1.

The type specimen of this species, constituting also the type of the genus *Shastasaurus*, was unfortunately represented by only a few posterior dorsal vertebrae and ribs, with one complete pubic bone and a portion of another. Though a considerable quantity of ichthyosaurian material has been known from the Upper Triassic of America, no other specimens have been discovered which seemed certainly to represent this specific type.

The species seems to be characterized by greater length of the vertebral centra anteroposteriorly than in any other species of *Shastasaurus*. The neural arches of the posterior dorsals are short and are considerably thickened but do not show the characters of *S. altispinus* or *S. careyi*.

The form of the pubis (fig. 148) is most nearly approached in *S. osmonti*. It differs from the form in that species in that the proximal end is broader and the posterior portion curves forward and inward toward the prominent posterior hook. In *S. osmonti* the proximal end of the pubis is narrower and is not upturned.

Associated with the type specimen of *S. pacificus* are three large discoidal elements, similar to those with the posterior limb of specimen 9608, referred to *S. osmonti*. They appear to have been slightly concave on the upper and lower surfaces. The discs are quite thick, and the edges are concave with an uneven or pitted surface. The form of these elements indicates that they were separated by a considerable body of cartilage. The discs resemble the phalanges of *Baptanodon*, but fail to show even the tendency to angularity seen in the proximal mesopodials of that form. Inasmuch as elements of this character are also found associated with the epipodial region in the types of *S. osmonti* and *D. perrini*, it is possible that they are proximal mesopodials. In *D. perrini* (no. 9082), the anterior and middle proximal carpals are however slightly angular. It is not improbable that in this species as in other forms of *Shastasaurus* the mesopodial and phalangeal elements were all reduced to the peripherally grooved or pitted discoidal form.

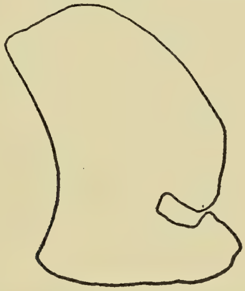


FIG. 148. *Shastasaurus pacificus* Merriam. Pubis, about ¼ natural size.

Though the characters of this form of *Shastasaurus* approach those of *S. osmonti*, and it may ultimately be necessary to unite them, no intermediate types are known. As long as the two forms can be distinguished the interests of classification are best subserved by recognizing them as distinct.

Shastasaurus altispinus Merriam

Shastasaurus altispinus Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 99, pl. 14, fig. 5, and pl. 15.

Vertebral centra not differing greatly in form and proportions from *S. osmonti*; neural spines of dorsal vertebrae very thick transversely. Excepting the blade-like anterior and posterior margins, they are nearly circular in cross-section. Distal end of spines hollowed by a groove-like anteroposterior excavation. Heads of dorsal ribs with two faces sharply turned away from each other; upper face usually more noticeably pitted than lower. The known podial limb elements with rounded and excavated or deeply pitted margins, but with a distinct notch on the outer side.

Very little is known of this species excepting the type specimen and a small amount of fragmentary material which may belong here. It seems to be fairly distinctly separated from *S. osmonti* and *S. alexandrae* with shorter and broader neural spines and less specialized rib heads. In *S. altispinus* the upper arches of the middle dorsal vertebrae are more than 20 per cent. higher than the centra, and in *S. osmonti* they are 10 per cent. shorter than the centra.

In *S. altispinus* the peculiar double facetted character of the heads of the dorsal ribs seems to be more strongly expressed than in any of the other species (pl. 18, figs. 3*a* and 3*b*). The lower face is generally less distinctly pitted than the upper, and was evidently in direct contact with the lower portion of the diapophysis. The upper face may be turned away from the lower face as much as thirty-five degrees. The surface of the upper face is generally quite distinctly concave. As is shown under the general discussion of the rib articulation of Triassic Ichthyosauria (p. 268) the adjustment of the rib to the vertebral centrum is in these forms quite different from that of the typical *Ichthyosaurus*.

From *S. careyi* this species differs in having longer vertebral centra and very much longer neural vertebral spines, with anteroposteriorly grooved instead of strongly convex terminal faces of the neural spines. The upper ends of the neural spines of the middle dorsal region are also much thicker than the middle portion of the arch in *S. careyi*. In *S. altispinus* a tendency to thicken the upper portion of the neural spines appears, but it is not developed as far as in *S. careyi*.

Two paddle elements occurring with the type specimen of this species both show sharp marginal notches (fig. 149) such as are not seen in any discoidal limb bones of *S. osmonti*. The peripheral face in these elements is concave and much roughened.

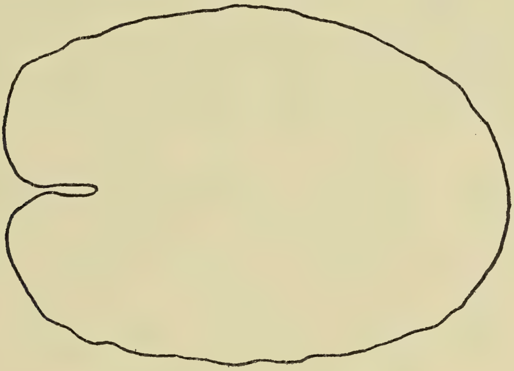


FIG. 149. *Shastasaurus altispinus* Merriam. Marginal element from mesopodial, metapodial, or phalangeal region, × $\frac{2}{3}$.

Shastasaurus careyi Merriam

Shastasaurus careyi Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 98, pl. 14, figs. 3 and 4.

Vertebral centra relatively high and short. Neural spines of dorsal vertebrae considerably thickened distally. Limb elements more abbreviated than in other species. Radius relatively large.

The type specimen (no. 9075, Univ. Calif. Col. Vert. Palae.) of this species consisted of two very large vertebrae and some rib fragments from the anterior dorsal or posterior cervical region. The diapophyses are short, and rudimentary parapophyses are present below them. The centra are relatively short anteroposteriorly. The dimensions of the centra in this specimen indicate that this form approached the size of the largest known species in the genus *Ichthyosaurus*.

MEASUREMENTS, No. 9075

Width of vertebral centrum from anterior dorsal or posterior cervical region	180 mm.
Height of centrum	*a* 160
Anteroposterior diameter of centrum	60

a Approximate.

A specimen (no. 9614; pls. 15 and 18) obtained from the Upper Triassic of Shasta County, California, in 1903 shows several characters of limbs and vertebrae not previously seen in any of the material from this region. It represents a large animal with greatly abbreviated propodial and epipodial limb elements. The vertebral centra are unusually short anteroposteriorly, while the short neural spines are nearly round in cross-section, and are much swollen at the distal end.

The characters of the limb elements (pl. 15) resemble somewhat those in *S. osmonti.* The humerus is much shorter and broader than in that species and is altogether the most abbreviated proximal limb segment known in any ichthyosaurian. The bone is also remarkably thick throughout, although the pectoral ridge shows relatively but little elevation compared with that of *S. osmonti.* The anterior edge is sharply emarginated as in the other species. On the distal end the faces of articulation are not distinctly separated by an angle as in *S. osmonti*, and the surface is considerably excavated. The radius is relatively large compared with the humerus. Both its length and width are greater compared with the corresponding dimensions of the humerus than in the other species. Its length is also less compared with its own width. Excepting the wide but rather sharply marked notch on the anterior margin, the outlines of the bone are gently rounded, in contrast to the somewhat angular form of the radius in *S. osmonti.* The posterior margin of the bone is convex instead of concave as in all other known Triassic ichthyosaurs, indicating the absence of a distinct gap between radius and ulna. Excepting the notched anterior side the whole border of the radius is sharply excavated by a continuous groove running around the margin.

MEASUREMENTS OF LIMB ELEMENTS, SPECIMEN 9614

Humerus, axial diameter	156 mm.
Humerus, greatest transverse diameter	212

Humerus, greatest thickness of proximal end	138 mm.
Humerus, greatest thickness of distal end	90
Radius, axial diameter	126
Radius, greatest transverse diameter	156

In specimen 9614, ten complete vertebrae are present in series, with the upper arches and ribs very little disturbed. The centra are large and are remarkably thin anteroposteriorly (pl. 18, fig. 5*a*). Judging from the position of the diapophyses they belong to the middle dorsal region. The centra are thinner than in any other species of *Shastasaurus*, unless it be *S. careyi*. The diapophyses are long and narrow. The anterior and posterior faces of the centra are evenly but deeply biconcave. The neural arches are relatively short, their height being considerably less than the height of the centra. The distal ends of the neural spines are much expanded and thickened, and the upper portion is slightly domed, instead of excavated as in *S. altispinus*. A horizontal cross-section of the upper portion of the neural spine is nearly circular, and at the upper end of the spine the transverse diameter is considerably greater than the corresponding diameter immediately above the zygapophyses. The zygapophysial facets are well developed although not very large.

MEASUREMENTS OF VERTEBRAE, SPECIMEN 9614

Height of centrum of vertebra from middle dorsal region	118 mm.
Transverse diameter of centrum	*a* 115
Anteroposterior diameter of centrum	34
Length of upper arch	79
Transverse diameter of neural spine behind anterior zygapophyses	25
Transverse diameter of neural spine at upper end	35

a Approximate.

Well preserved ribs (pl. 18, fig. 6) are present with each of the vertebral centra with this specimen. The form of these ribs is in general similar to that of the ribs in *S. osmonti*, excepting that the shaft and head are apparently somewhat heavier. The posterior side of the shaft is strongly grooved in the proximal half. The distal portion has been broken away in all cases. As in *S. osmonti* and *S. altispinus*, the upper portion of the articular face of the rib is turned rather sharply outward from the plane of the lower portion of the face.

Of the known species this form is evidently nearest to *S. careyi* and *S. altispinus*. Though the vertebrae cannot be compared closely with the known type of *S. careyi*, owing to their not belonging in the same region of the column, they seem to be somewhat thinner anteroposteriorly. Their fore-and-aft diameter equals about 29 per cent. of the height of the centrum while in *S. careyi* it equals about 37 per cent.

In *S. altispinus* vertebral centra from a region of the column corresponding closely to that represented in specimen 9614 are much thicker than in this specimen. Also, the neural arches are relatively almost twice as long, and are much less expanded distally.

Considering that specimen 9614 represents a different part of the vertebral column from that seen in the type of *S. careyi*, it is not improbable that it represents the same specific type or at least a closely allied species. The extremely specialized character of the anterior limb found here one would expect to find in *S. careyi* of all the known species, as it is the latest and the largest of the several types.

Mixosauridae of Uncertain Position

Cymbospondylus (?) nordenskiöldii (Hulke)

Ichthyosaurus nordenskiöldii Hulke, Beihang. K. Svenska Vet. A. Handlingar, Bd. 1, no. 1.

Mixosaurus nordenskiöldii (Dames), Sitzb. der Acad. der Wiss., Berlin, 1895, p. 1047.

To this species Hulke referred a number of vertebrae and ribs obtained by A. E. Nordenskiöld in the Triassic of Saurie Hook, Spitzbergen.

The specimens referred to this species represent a smaller form than *C. (?) polaris*. The vertebrae present represent the thoracic and caudal regions. The dorsal vertebrae (2*a*) described by Hulke are subcircular, slightly angular, and approaching a hexagonal form in anteroposterior profile, the greatest width or transverse diameter nearly equaling the height. The height is about 1.65 in. The anteroposterior diameter is .35 in. They show anterior and posterior articular surfaces which are unequally hollow. On one centrum the diapophysial articular surface is apparently confluent with the neurapophysial articular surface. The interval between the diapophysis and parapophysis exactly corresponded to the interval between the tuberculum and capitulum of a rib near by. As it is described, this vertebra might represent a posterior cervical or an anterior dorsal of either a shastasaurine or an ichthyosaurine form.

The caudal vertebrae referred to this species were recognized by Hulke as differing markedly from the caudals of the typical *Ichthyosaurus*, but their reference to an ichthyosaurian seemed unavoidable owing to their association with unmistakable tabular, polygonal ossicles plainly belonging to an ichthyosaurian paddle. The caudal centra were characterized by having a vertical diameter relatively long as compared with the transverse diameter. The articular faces of the caudals were characterized by a small but deep pit immediately below the middle.

The dimensions of a caudal (series 2, *d* Hulke) were: anteroposterior diameter, .3 in.; vertical diameter, about 1 in.; horizontal transverse diameter, .6 in.

The caudal centra of this species in their general form resemble the centra of the distal third of the caudal region in *Cymbospondylus* (see pl. 9, figs. 8*a* and 8*b*), and of other shastasaurine forms, and do not differ greatly from those of *Mixosaurus*. (See fig. 124, p. 320.)

Two fragments forming part of the snout of a reptile were found by Hulke in the Nordenskiöld collection from Spitzbergen, and were considered as probably belonging in the genus *Ichthyosaurus*. The anterior teeth were smaller than the posterior ones, and were set in an open continuous groove. The posterior teeth were found to occupy separate sockets, the dentary groove being interrupted in this region by transverse partitions between the teeth. All of these teeth showed a simple oblong cross-section through the neck, the anteroposterior diameter being to the transverse as 2:1 or in some cases 2.5:1. A portion of a crown protruding showed relatively coarse longitudinal fluting.

In later examination by Dames (1895) of the specimens studied by Hulke, the statements of Hulke were substantiated, and attention was called to the remarkable similarity of these specimens to *Mixosaurus ?* of the European Middle Trias. Dames noted several minor differences between the dentition of the Spitzbergen form and that of *M.* (*?*) *atavus*. In *M.* (*?*) *atavus* the cross-sections of the teeth were stated by Dames to be nearly round, and the partitions between the alveoli weak. In the Spitzbergen form the cross-sections are relatively narrow transversely, and the partitions between the alveoli are strong. According to the observations of the writer the most posterior teeth of *M.* (?) *atavus* may show some lateral compression.

Taking everything into consideration, the affinities of Hulke's *I. nordenskiöldii* seem closer with *Cymbospondylus* than with any other known genus. The Spitzbergen form differs from *Mixosaurus,* particularly in the nature of the rib articulation in the cervical or anterior dorsal vertebrae.

In the great excess of their vertical diameter, the caudal vertebrae of *C.* (?) *nordenskiöldii* were stated by Hulke to resemble a vertebra found by Sir. Ed. Belcher, in 1852, on Exmouth Island, lat. 77° 16′ N., long. 96° W. This specimen was figured by Owen in the appendix (p. 389) to Belcher's "Last of the Arctic Voyages."

Cymbospondylus (?) *polaris* (Hulke)

Ichthyosaurus polaris Hulke, Bihang K. Svenska Vet. Ak. Handlingar, Bd. 1' no. 9.

Ichthyosaurus (*Mixosaurus*) *polaris* (Dames), Sitzb. der Acad. der Wiss., Berlin, 1895, p. 1405.

Ichthyosaurus? (*Shastasaurus?*) *polaris* (Merriam), Univ. Calif. Publ. Geol., vol. 3, pp. 87 and 88.

Shastasaurus polaris (Yakowlew), Verh. d. Kais. Russ. Min. Ges., Bd. 40, p. 194.

This species was described by Hulke from fragmentary material obtained by A. E. Nordenskiöld in the Triassic of Spitzbergen. Yakowlew (1902, 1) referred a vertebra to this form. Hulke studied two vertebral series. One series included eight vertebrae, the other three. In the series of eight vertebrae the outline of one of the centra is described as roughly that of a rather narrow, long horseshoe. The dimensions of this centrum were as follows: height, 3.9 in.; transverse diameter, 2.7 in.; anteroposterior diameter, 1.4 in. About half way down on the side of one centrum was an oblong rib facet 1.2 in. long and .4 in. wide. The facet was slightly contracted at the middle and extended obliquely downward toward the anterior border of the centrum.

The anterior and posterior faces of the centrum were said to be deeply concave, but relative to the whole area the extent of the concavity was small, and for some distance below the neural canal the surface was nearly plane.

The vertebrae present in the series of eight centra Hulke considered as representing the posterior dorsal or the anterior caudal region. The writer (1902, 2, p. 88) suggested that they resemble the posterior dorsals of *Shastasaurus*. The narrow form of the centra favors somewhat Hulke's suggestion regarding their position in the anterior caudal region, but the long, narrow rib articulation is more like that of posterior dorsals in the shastasaurine group. The limited area of deep concavity on the anterior and posterior faces suggests the characters of *Cymbospondylus petrinus*, in which the posterior dorsals are also relatively narrow (pl. 9, figs. 2 and 3).

The three consecutive centra of the second vertebral series were much compressed laterally and had short rib facets. They may have represented caudals.

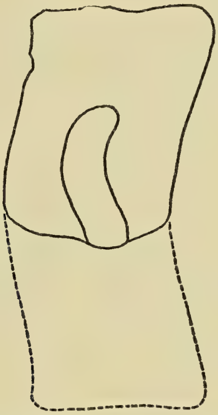


Fig. 150. *Cymbospondylus* (?) *polaris* (Hulke). Middle dorsal vertebra, × ½. (After Yakowlew.)

Judging from the available material of this species it belongs in the shastasaurine group. It is not possible to make certain of the genus to which it belongs. The suggestion of Yakowlew and the writer regarding its affinities with *Shastasaurus* were justified in the light of the information at hand, but with a better knowledge of the genus *Cymbospondylus* it appears that *polaris* might be placed in that genus with more reason than could be advanced for referring it to *Shastasaurus*.

Cymbospondylus (?) *natans*, n. sp.

A perfectly preserved humerus (no. 9873, see pl. 13, figs. 1*a* and 1*b*) from the Triassic of the West Humboldt Range of Nevada differs so much from the humerus of *Cymbospondylus petrinus* that its characters are not covered by the description of that species, and possibly not even by the genus *Cymbospondylus*. In some respects this specimen approaches the genus *Mixosaurus* more closely than does the typical *Cymbospondylus*.

As indicated by the following measurements the humerus is relatively short and broad and represents a somewhat smaller form than the typical *Cymbospondylus petrinus*.

MEASUREMENTS OF HUMERUS, No. 9873

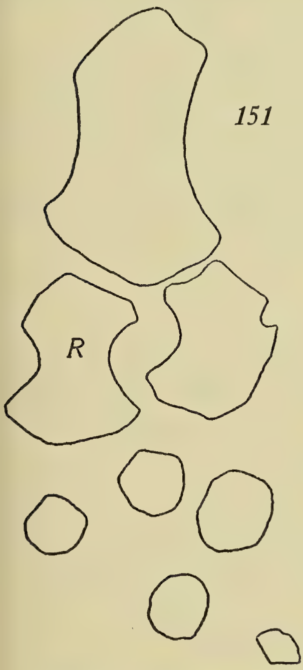
Greatest length	53 mm.
Greatest width of distal end	38
Width of median or shaft region	31
Greatest thickness of distal end	11

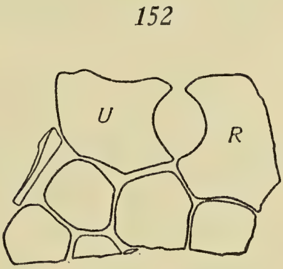
The shaft of the humerus is much shorter than in *C. petrinus*, and is broadened by an expansion of the anterior margin. The posterior half of the proximal end shows a well developed hemispherical articular face which grades into a broad, concave articular face immediately anterior to it. On the anterior side of the lower face of the proximal end there is a short but well marked pectoral ridge. On the distal end, the two articular faces are distinctly separated by a prominent angle. The posterior articular face is much shorter than the anterior. The anterior articular face extends over the anterior distal angle and along the anterior margin for about three-fourths of the distance to the proximal end. The apparent extension of this face over the anterior border probably represents no more than a cartilage covered surface. The anterior articular face is concave transversely and convex in the direction normal to the plane of the distal end. The posterior face is convex transversely and concave in the direction normal to the plane of the end.

To this species the writer is inclined to refer tentatively a small specimen (no. 11229; fig. 152) representing a portion of the epipodial and mesopodial region of a limb, accompanied by a number of rather slender ribs. The epipodial elements appear to be less constricted than in *Cymbospondylus petrinus*, and have much the same form as *Mixosaurus cornalianus*. The element which appears to represent the radius was evidently not deeply concave anteriorly, and the ulna was possibly not constricted medially.

The elements of the mesopodial region are angular instead of rounded. There are in the proximal row three elements closely resembling the radiale, intermedium and ulnare of *Mixosaurus.* Behind the ulnare there is a portion of a third element which may represent the pisiform of *Mixosaurus.* Articulating with the ulnare there are two elements in the distal row of the carpus. The anterior of these two shows a small contact with the intermedium. The distal end of the intermedium is not complete.

With this species there may also be placed tentatively several series of caudal vertebrae representing a primitive type of caudal fin. One of these specimens (no. 10624; see pl. 10, fig. 1) is a part of an individual somewhat larger than that represented by the humerus standing as the type of this species. Other specimens showing much the same type of caudal vertebrae as those in no. 10624 belong to smaller individuals.





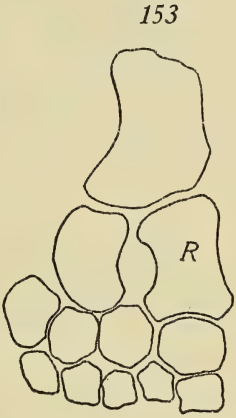


FIG. 151. *Cymbospondylus petrinus* Leidy. Proximal portion of anterior limb, × $\frac{1}{9}$.
FIG. 152. *Cymbospondylus* (?) *natans*, n. sp. A portion of an anterior limb, × $\frac{1}{2}$.
FIG. 153. *Mixosaurus cornalianus* (Bassani.) Proximal portion of an anterior limb, × $\frac{1}{2}$. (Adapted from Repossi.)

The vertebral centra in the caudal series mentioned above are high and narrow. They vary somewhat in anteroposterior diameter in different specimens. On specimen 10624 well marked diapophyses are present. The anterior and posterior articular faces are not well shown, but as nearly as can be determined they are not deeply concave from the margins inward, but are probably of the form seen in the caudals of *Cymbospondylus petrinus* (pl. 9, fig. 8*b*).

The upper arches are greatly elongated, the height amounting to more than two and one-half times that of the centrum in one case. Though much elongated the neural arches are not greatly compressed laterally. Zygapophysial notches are noticeable particularly on the posterior margins of these arches.

The lower arches are also very long, their length almost equaling that of the neural arches. Their attachment to the centra cannot be clearly made out in every case. In one instance a suture between an articular head of a lower arch and the centrum can be clearly seen. In other cases the lower arches may possibly be fused with the centra, as in the mosasaurian genus *Clidastes*.

Ichthyosaurus Koenig

Single articulation of presacral ribs found only in the posterior dorsal region. Hypocentral elements of caudal region not meeting to form Y-shaped arches. Distal region of caudal series sharply decurved. Lateral zygapophysial faces united to form single anterior and posterior facets. Scapula narrow distally. Pelvic element much reduced. Epipodial elements short, rarely separated by a cleft. Phalangeal elements short, with angulated or rounded margins. Maxillary relatively short compared with the premaxillary. Orbits very large. Postorbital bar narrow. Teeth numerous, isodont, situated in open grooves.

Several of the Triassic ichthyosaurian forms which are represented by fragmentary material seem to stand nearer to *Ichthyosaurus* than to any of the typical Triassic genera, and may be referred tentatively to that genus. It is not improbable that some of these when represented by better material may be shown to be generically distinct from *Ichthyosaurus*. On the other hand it is to be presumed that *Ichthyosaurus* was in existence in late Triassic time, and there appears to be no reason why it should not be represented in the formations of that period in Europe where it was so abundant in the early Jurassic.

Ichthyosaurus carinatus Sauvage

Ichthyosaurus carinatus Sauvage, Ann. Sc. Geol., t. 7, art. 6, 1876.

From the Rhaetic of the vicinity of Autun, France.

According to Sauvage this species is large, and is characterized by the flattening of the centrum and the carina of the inferior face of the centrum in the middle dorsal region. The anterior dorsal centra are oval; the articular faces are deeply concave; the diapophyses and parapophyses are widely separated.

Measurements of an Anterior Dorsal Centrum

Anteroposterior diameter of centrum	60 mm.
Height of centrum	160
Width of centrum	145

Length, 100; height, 266; width, 242.

Measurements of a Middle Dorsal Centrum

Anteroposterior diameter of centrum	57 mm.
Height of centrum	168
Width of centrum	173

Length, 100; height, 295; width, 303.

The specimens figured by Sauvage (1883, pl. 8) seem to represent a form which is generically closely allied if not identical with *Ichthyosaurus*.

Ichthyosaurus (?) *rheticus* Sauvage

Ichthyosaurus rheticus Sauvage, Ann. Sc. Geol., t. 7, art. 6.
Rachitrema pellati Sauvage, Ann. Sc. Geol., t. 14, art. 3, p. 5; and Bull. Soc. D'Hist. Nat. D'Autun, t. 16, p. 315.

From the Rhaetic of the vicinity of Autun, France.

This is a large species in which the centra of the dorsal vertebrae are much higher than long (anteroposterior diameter or length, 100; height, 234; width, 243). The centra are strongly biconcave, the concavity commencing at the margin. There is no ridge on the inferior face of the centra. The diapophyses and parapophyses are large and are nearly in contact on the specimens described.

Of this species there was originally described a small amount of material representing vertebrae, ribs, a portion of a scapula, and a femur. Other material originally described under the name *Rachitrema pellati* has recently been referred by Sauvage (1903) to *I.* (?) *rheticus*. Von Huene (1902, p. 71) has suggested that *Rachitrema* is an ichthyosaurian rather than a dinosaur.

The material which has been referred to *I.* (?) *rheticus* and to *Rachitrema pellati* by Sauvage, and was figured by him (1883), appears to represent an ichthyosaurian having its closest affinities with the Ichthyosaurinae. The vertebra of *I.* (?) *rheticus* figured by Sauvage (1883, pl. 8, fig. 4*a*) evidently represents a middle dorsal in which the diapophyses are almost in contact with the large parapophyses (fig. 154). In no representative of the shastasaurine group are parapophyses known behind the region in which the diapophysial articular faces become separated from the neurapophysial faces. The upper arch referred to *Rachitrema pellati* is however somewhat more primitive in its characters than the corresponding arches of the Jurassic ichthyosaurs.

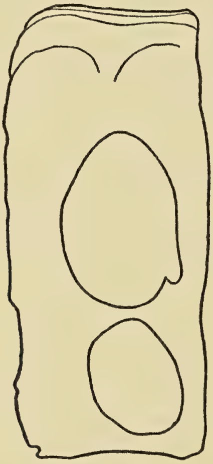


FIG. 154. *Ichthyosaurus* (?) *rheticus* Sauvage. Outline, side view, of middle dorsal vertebral centrum, slightly reduced. (Adapted from Sauvage.)

Ichthyosaurus (?) *hectori* Lydekker

Ichthyosaurus australis Hector, Trans. New Zealand Inst., vol. 6, p. 355.
Ichthyosaurus hectori Lydekker, Catlg. Foss. Rept. Brit. Mus., pt. 2, p. 113.

In the collections of fossil reptilia of New Zealand examined by Hector, the genus *Ichthyosaurus* was represented by a single vertebral centrum, in a micaceous sandstone from the rocks of Mount Potts, in the Rangitata district of the province of Canterbury. The beds were said to be identical with strata that in other parts of the colony were considered to be Triassic.

The name *I. australis,* which Hector first used for this form, having been used for a Cretaceous species from Australia, Lydekker named the species after Hector.

So little is known of this form that no suggestion regarding its affinities can be made.

Ichthyosaurus, sp.

To this genus there have been referred a number of ichthyosaurian remains obtained in Rhaetic beds at Aust Cliff near Bristol, England. This material was referred to *Ichthyosaurus* by Phillips (1871). Lydekker (1889) suggested the resemblance of a tooth from this locality to the type of *I. lonchiodon.* Von Huene (1902) mentions numerous vertebrae, and a large snout fragment of the size of *I. platyodon* and *trigonodon* from the beds at Aust Cliff.

Date of issue:
September 30, 1908

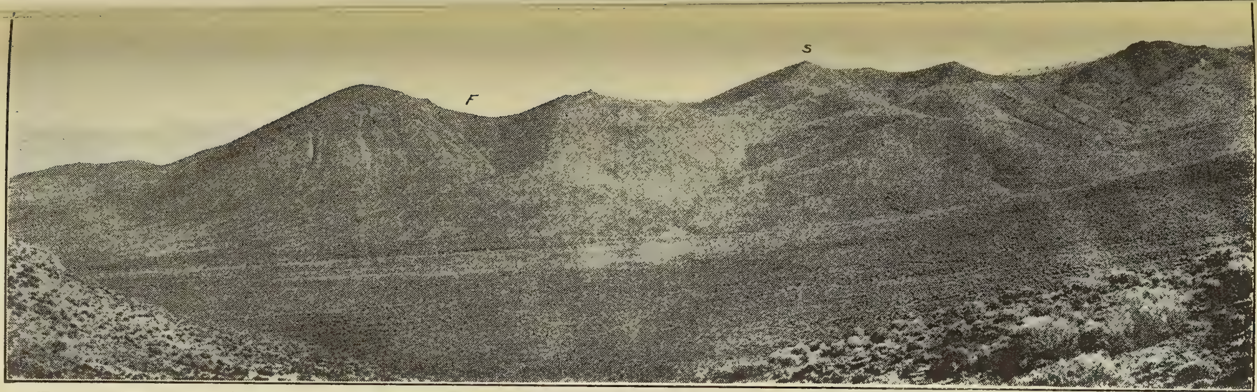


Fig. 1. Exposure of Middle Triassic limestones on the south fork of American Cañon, West Humboldt Range, Nevada. Limestones extending from Saurian Hill (*S*) to the end of the ridge beyond Fossil Hill (*F*).

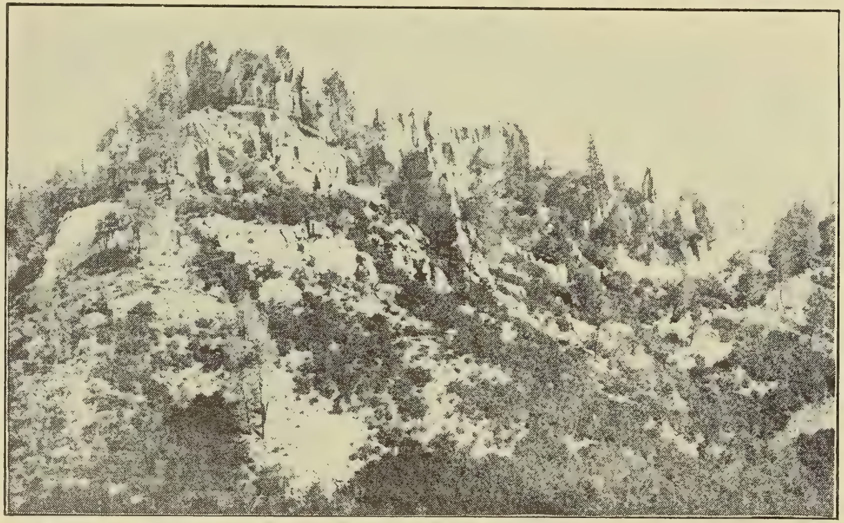


Fig. 2. Exposures of Upper Triassic, Hosselkus Limestone, on Brock Mountain, Shasta County, California. The massive upper limestones are conspicuously pinnacled. The more shaly beds of the lower horizon are less conspicuous, and are largely covered with thick brush.

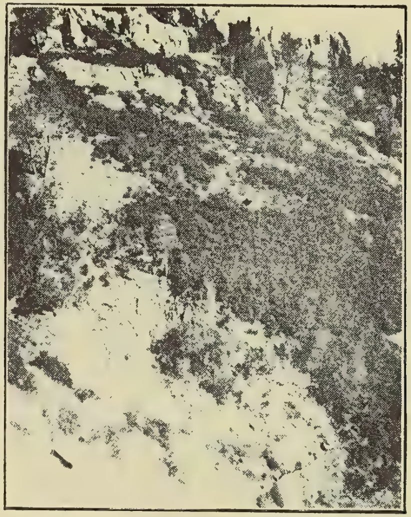


Fig. 3. Detail from fig. 2 showing the contorted shaly limestones of the lower horizon from their upper contact down almost to the Pit Shale.

EXPLANATION OF PLATE 2

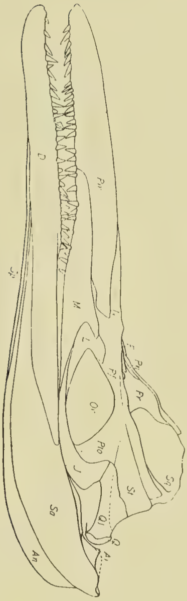
Cymbospondylus petrinus Leidy

Lateral view of skull, no. 9950, $\times\frac{2}{15}$

From the Middle Triassic of West Humboldt Range, Nevada

Legend

Pm, premaxillary
M, maxillary
N, nasal
L, lachrymal
F, frontal
Pn, pineal foramen
Pr, parietal
Pf, prefrontal and postfrontal
Pto, postorbital
J, jugal
Or, orbit
Sq, squamosal
St, supratemporal
Q, quadrate
Qj, quadratojugal
Ar, articular
Sa, surangular
An, angular
D, dentary
Sp, splenial


D
Pmx
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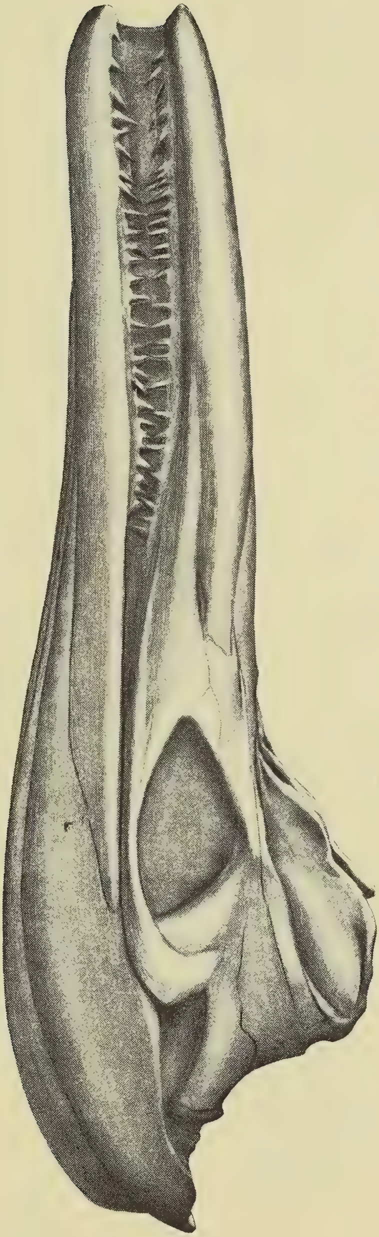


EXPLANATION OF PLATE 3

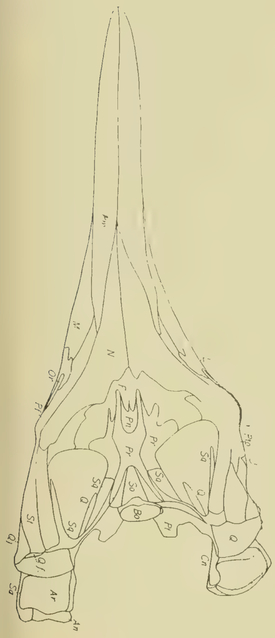
Cymbospondylus petrinus Leidy

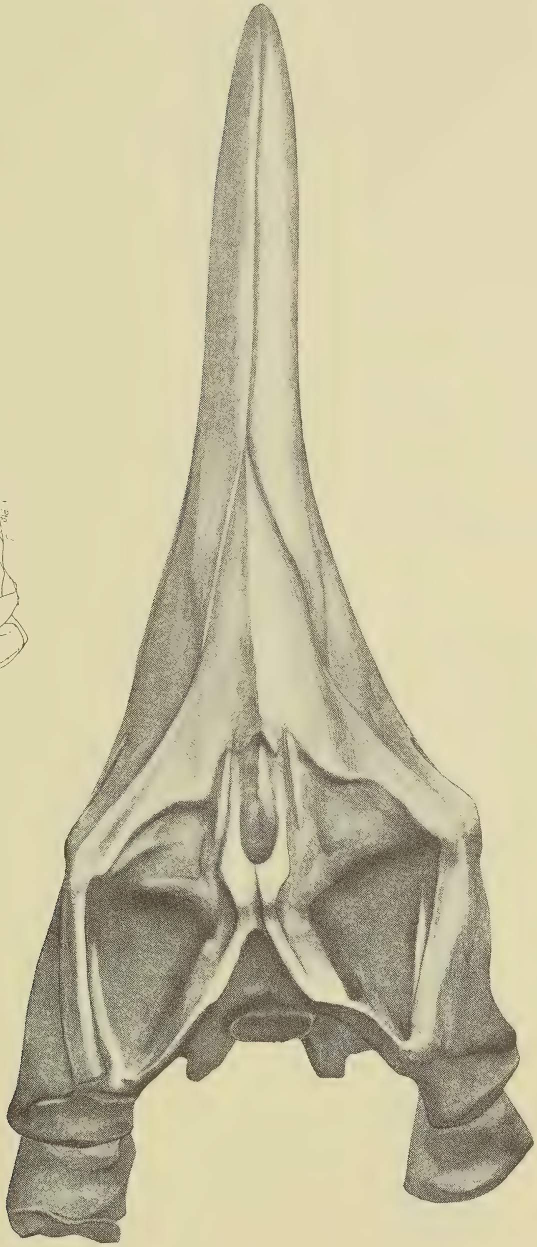
Superior view of skull, no. 9950, $\times \frac{2}{15}$

From the Middle Triassic of West Humboldt Range, Nevada

LEGEND

Pm, premaxillary
M, maxillary
N, nasal
L, lachrymal
Or, orbit
F, frontal
Pn, pineal foramen
Pr, parietal
Pf, prefrontal and postfrontal
Pto, postorbital
J, jugal
Sq, squamosal
St, supratemporal
Qj, quadratojugal
Q.f., quadrate foramen
Q, quadrate
So, supraoccipital
Bo, basioccipital
Pt, pterygoid
Ar, articular
Sa, surangular
An, angular
Cn, coronoid
Pt, pterygoid


Pm
M
N
Or
Pf
F
Pm
Pr
Pr
Sa
So
So
Sa
Q
Q
Sq
Bo
Pt
St
Sa
Qj
Q.j.
Sa
Ar
An
Pto
Q
Cn



EXPLANATION OF PLATE 4

Cymbospondylus petrinus Leidy

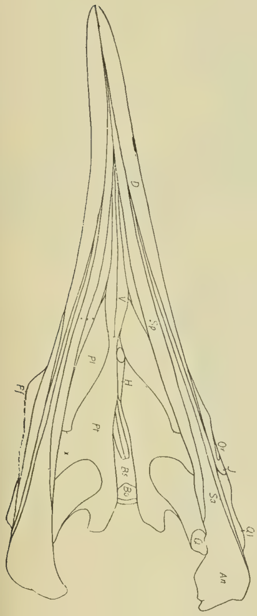
Inferior view of skull, no. 9950, × $\frac{2}{15}$

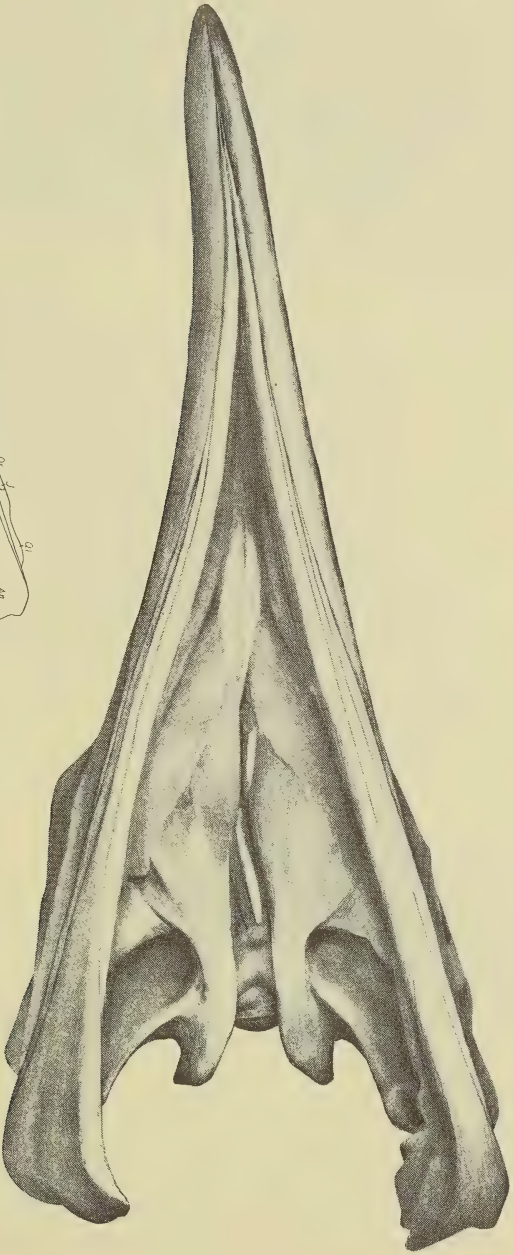
From the Middle Triassic of West Humboldt Range, Nevada

Legend

D, dentary
Sp, splenial
Sa, surangular
A, angular
V, prevomer?
Pl, palatine
Pt, pterygoid
X, ectopterygoid?

H, hyoid
Bs, basisphenoid
Bo, basioccipital
Q, quadrate
Qj, quadratojugal
J, jugal
Or, orbit
Pf, prefrontal and postfrontal


D
V
Sp
Pl
Pf
H
Pt
x
Or
J
Bs
Bo
Sa
Q
Ql
An



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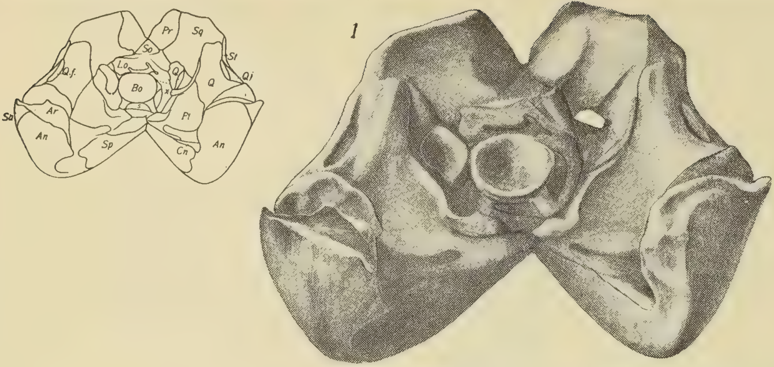
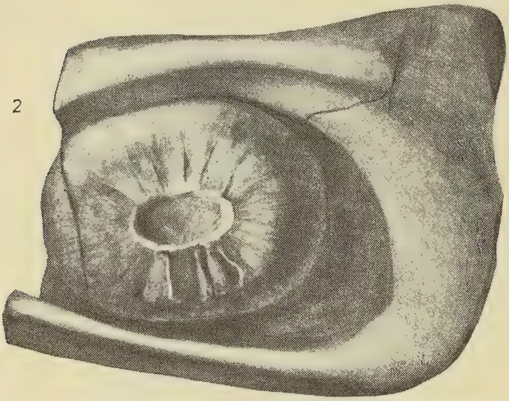


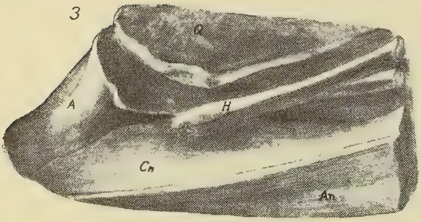
Posterior view of skull, no. 9950, $\times\frac{2}{15}$

2



Orbital region showing complete sclerotic ring, no. 9954, $\times\frac{2}{9}$

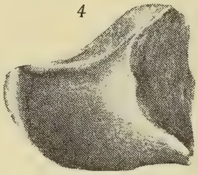
3



Inner side of posterior end of left ramus of the mandible, no. 9913, $\times\frac{2}{9}$

A, articular; *Cn*, coronoid; *An*, angular; *H*, hyoid; *Q*, quadrate

4



Superior view of right articular, no. 9913, $\times\frac{2}{9}$

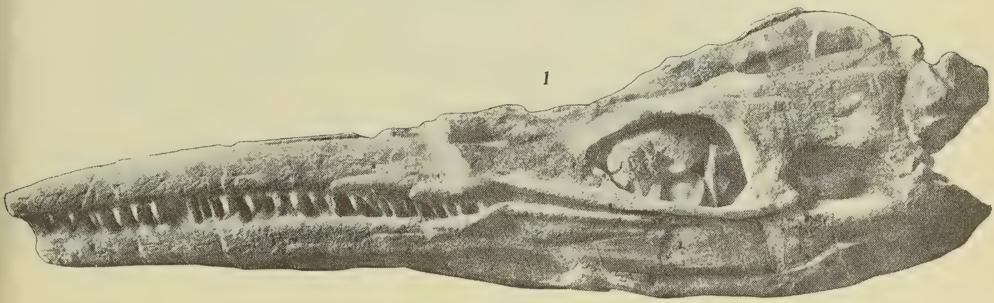
Cymbospondylus petrinus Leidy

From the Middle Triassic of West Humboldt Range, Nevada

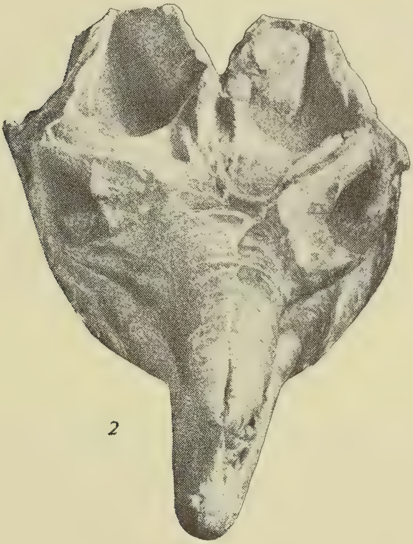
Pr, parietal
Sq, squamosal
St, supratemporal
Qj, quadratojugal
Q, quadrate
Q.f., quadrate foramen

So, supraoccipital
Lo, lateral occipital (?)
Bo, basioccipital
S, basisphenoid
Pt, pterygoid
X, indeterminate (stapes?)

Ar, articular
Sa, surangular
An, angular
Sp, splenial
Cn, coronoid



Lateral view of cranium, no. 9913, about $\frac{1}{10}$ of natural size



Anterior view of cranium, no. 9950, a little less than $\frac{2}{15}$ of natural size

Cymbospondylus petrinus Leidy

From the Middle Triassic of West Humboldt Range, Nevada

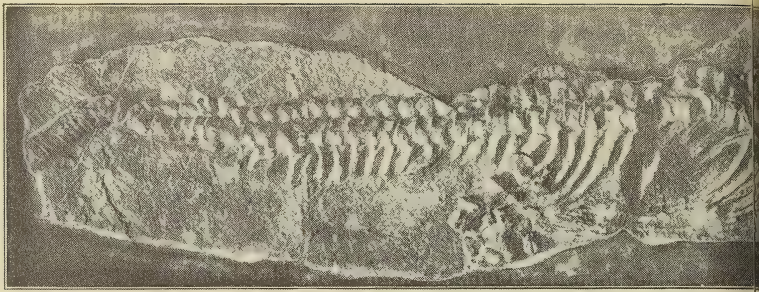


Fig. 2. *DELPHINOSAURUS PERR*

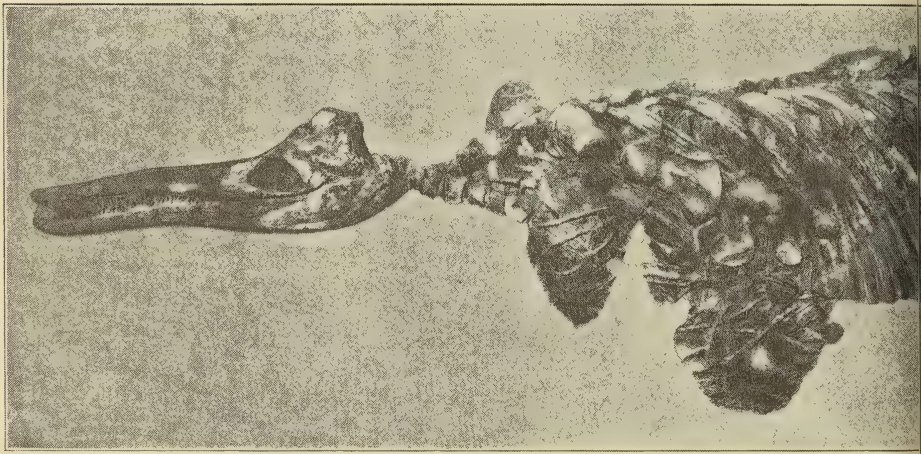


Fig. 1.

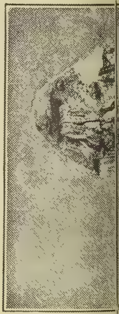
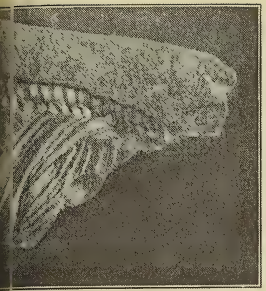
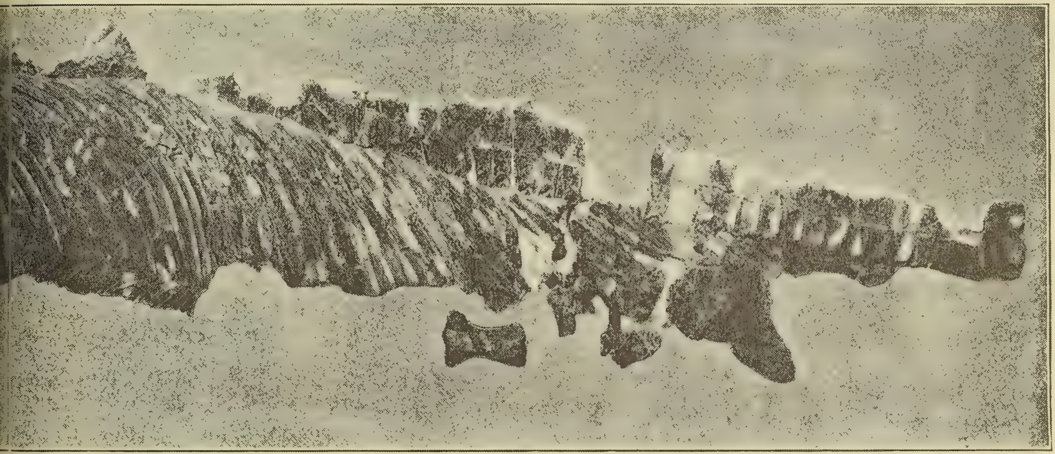


Fig. 1. *Cymbospondylus petrinus* Leidy. Photograph of mounted specimen, no. 9950, about $\frac{1}{24}$ of natural size. Restoration is limited to the distal portion of some of the ribs. From the Middle Triassic of West Humboldt Range, Nevada.

Fig. 2. *Delphinosaurus perrini* Merriam. Type specimen, no. 9119, a little less than $\frac{1}{12}$ of natural size. From the Upper Triassic of Shasta County, California.

Fig. 3. *Delphinosaurus perrini* Merriam. Specimen 10998. About $\frac{1}{15}$ of natural size. From the Upper Triassic of Shasta County, California.





US PETRINUS Leidy

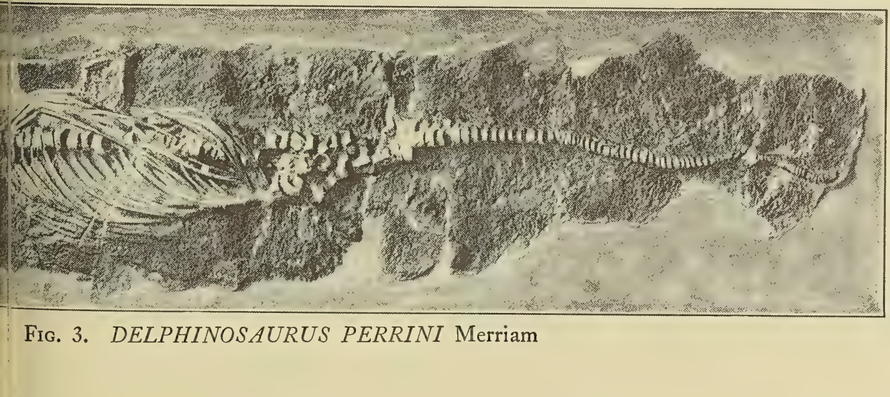


Fig. 3. *DELPHINOSAURUS PERRINI* Merriam

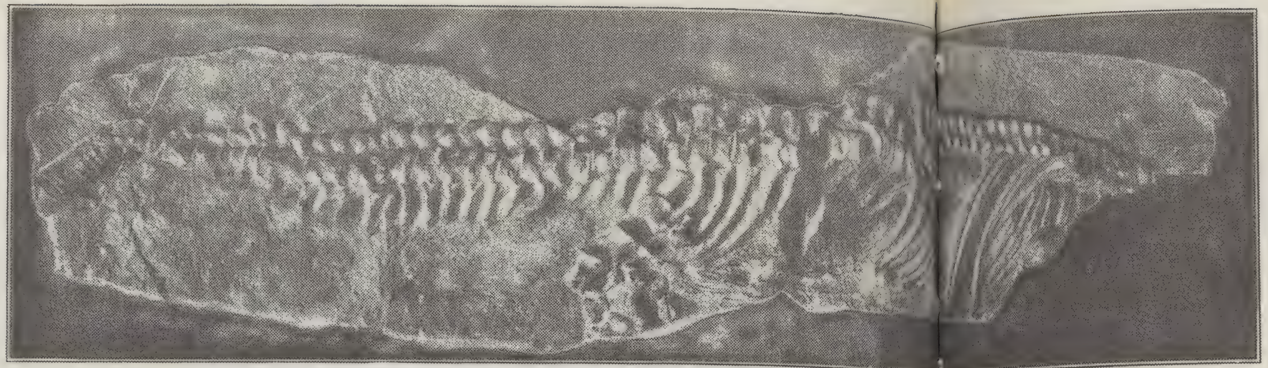


Fig. 2. *DELPHINOSAURUS PERRIN*

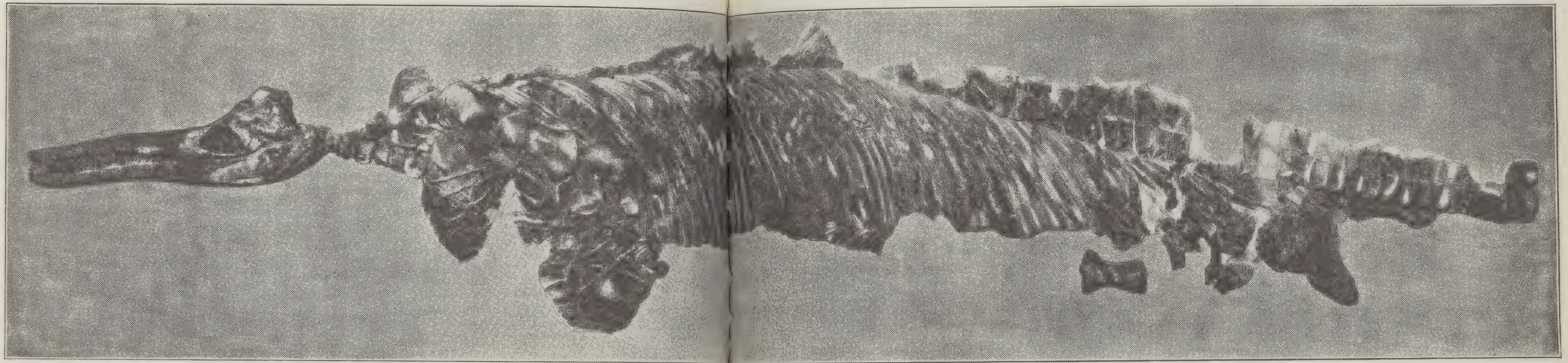


Fig. 1. *C DYLUS PETRINUS* Leidy

Fig. 1. *Cymbospondylus petrinus* Leidy. Photograph of mounted specimen, no. 9950, about $\frac{1}{24}$ of natural size. Restoration is limited to the distal portion of some of the ribs. From the Middle Triassic of West Humboldt Range, Nevada.

Fig. 2. *Delphinosaurus perrini* Merriam. Type specimen, no. 9119, a little less than $\frac{1}{12}$ of natural size. From the Upper Triassic of Shasta County, California.

Fig. 3. *Delphinosaurus perrini* Merriam. Specimen 10998. About $\frac{1}{15}$ of natural size. From the Upper Triassic of Shasta County, California.

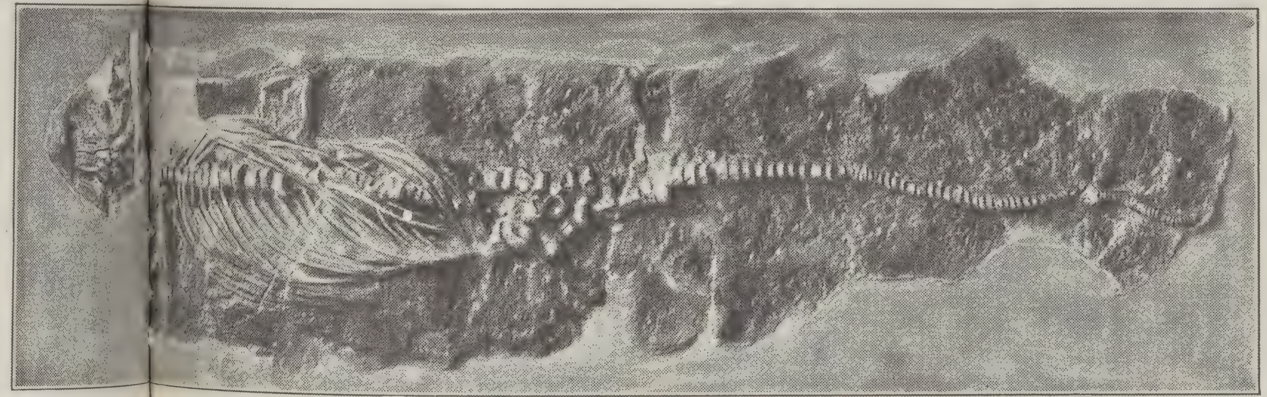


Fig. 3. *DELPHINOSAURUS PERRINI* Merriam

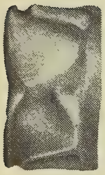
EXPLANATION OF PLATE 8

Cymbospondylus petrinus Leidy

From the Middle Triassic of West Humboldt Range, Nevada

All figures three-tenths of natural size

Fig. 1*a*–1*d*. Atlas and axis, no. 9943.
  1*a*, axis, inferior view, anterior face to right.
  1*b*, atlas, anterior view.
  1*c*, atlas, superior view, anterior face to right.
  1*d*, atlas, lateral view, anterior face to left.
Fig. 2. Atlas and axis, no. 9154, superior view.
Fig. 3. Atlas and axis, no. 9913, inferior view.
Fig. 4. Upper arch of cervical vertebra, no. 9943, anterior view.
Fig. 5. Atlas, lateral view, no. 9913, anterior face to right.
Fig. 6. Axis, lateral view, no. 9950.
Fig. 7*a*–7*c*. Third cervical, no. 9950.
  7*a*, lateral view; 7*b*, anterior view; 7*c*, upper arch.
Fig. 8. Fifth cervical, no. 9950.
Fig. 9. Sixth cervical, no. 9950.
Fig. 10. Anterior dorsal, no. 9950.
Fig. 11. Middle dorsal, no. 9154.
Fig. 12. Middle dorsal, no. 8128.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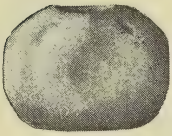
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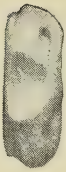
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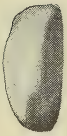
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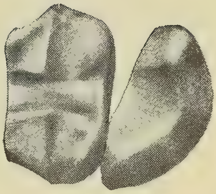
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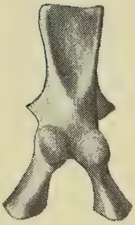
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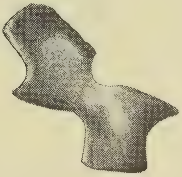
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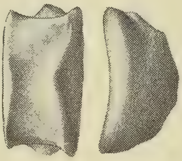
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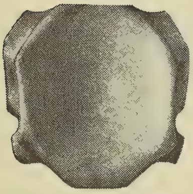
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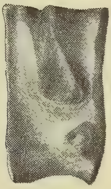
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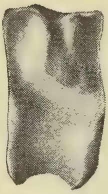
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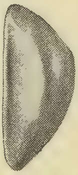
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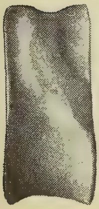
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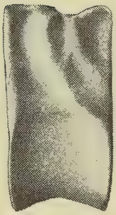
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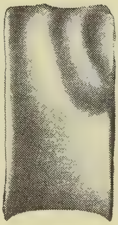
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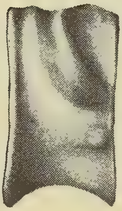
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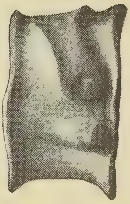
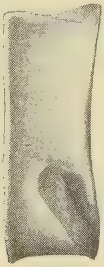

8

FIG. 1. Posterior dorsal vertebra, no. 9950.

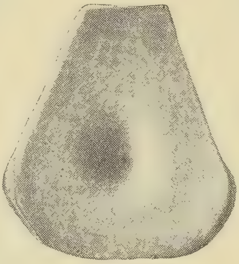
FIG. 2. Posterior dorsal vertebra, no. 8128.

FIG. *3a* and *3b*. Posterior dorsal vertebra, no. 8128, situated somewhat farther back in the series than the centrum represented by fig. 2.

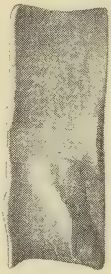
3a, anterior view; *3b*, lateral view.



3b



3a



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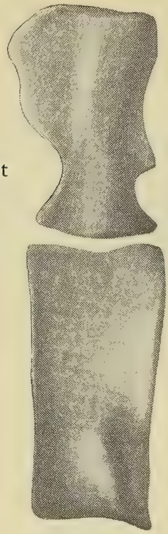


1

FIG. 4. Anterior caudal vertebra, no. 9947.

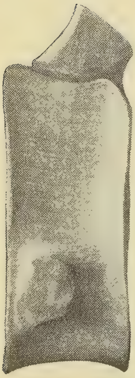
FIG. 5. Middle caudal vertebra, anterior to bend of tail, no. 9947.

FIG. 6. Middle caudal vertebra, situated at the anterior end of caudal flexure, no. 9947.

FIG. 7. Posterior caudal vertebra, situated at about the middle of the caudal flexure, no. 9947.

FIG. 8*a* and 8*b*. Posterior caudal vertebra, situated near the posterior end of the tail, no. 9947.

8*a*, lateral view, with chevron; 8*b*, anterior view.



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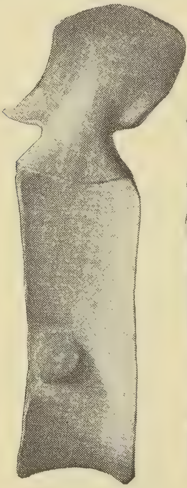

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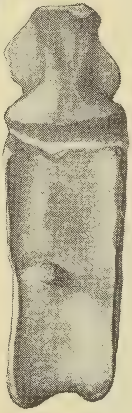

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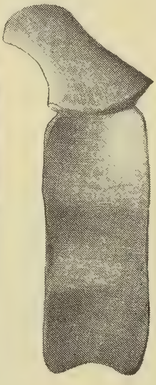

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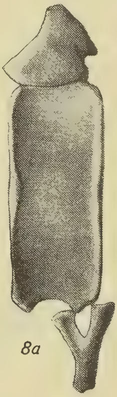

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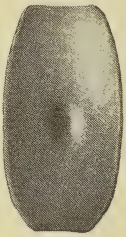


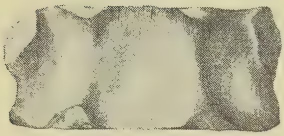
8b

Cymbospondylus petrinus Leidy

From the Middle Triassic of West Humboldt Range, Nevada

All figures three-tenths of natural size

2a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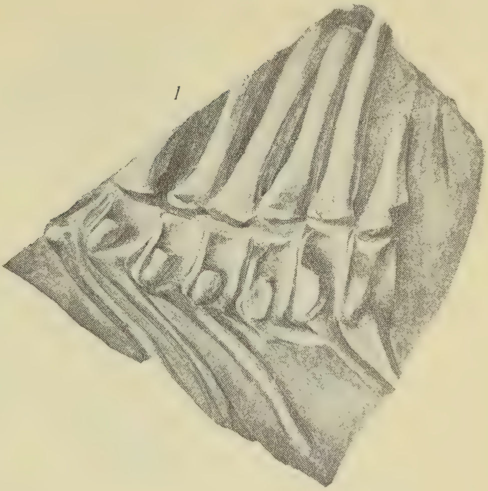
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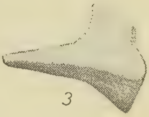
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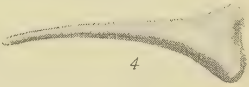
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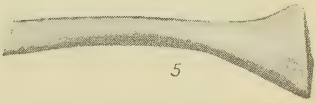
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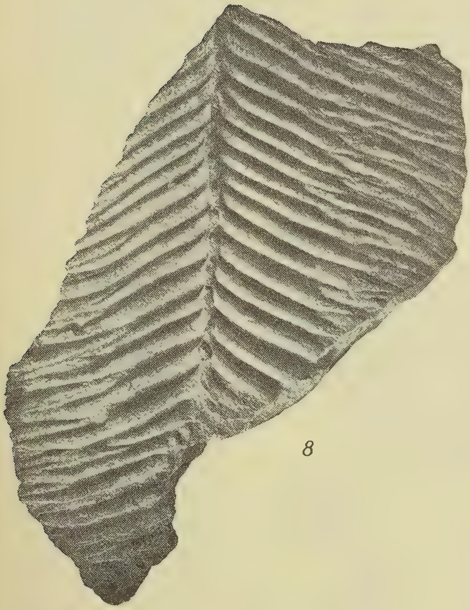
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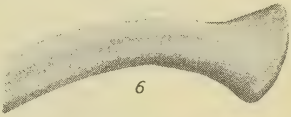
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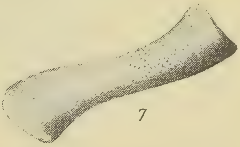

7

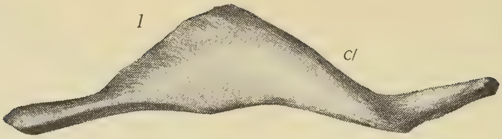
All specimens from the Middle Triassic of West Humboldt Range, Nevada

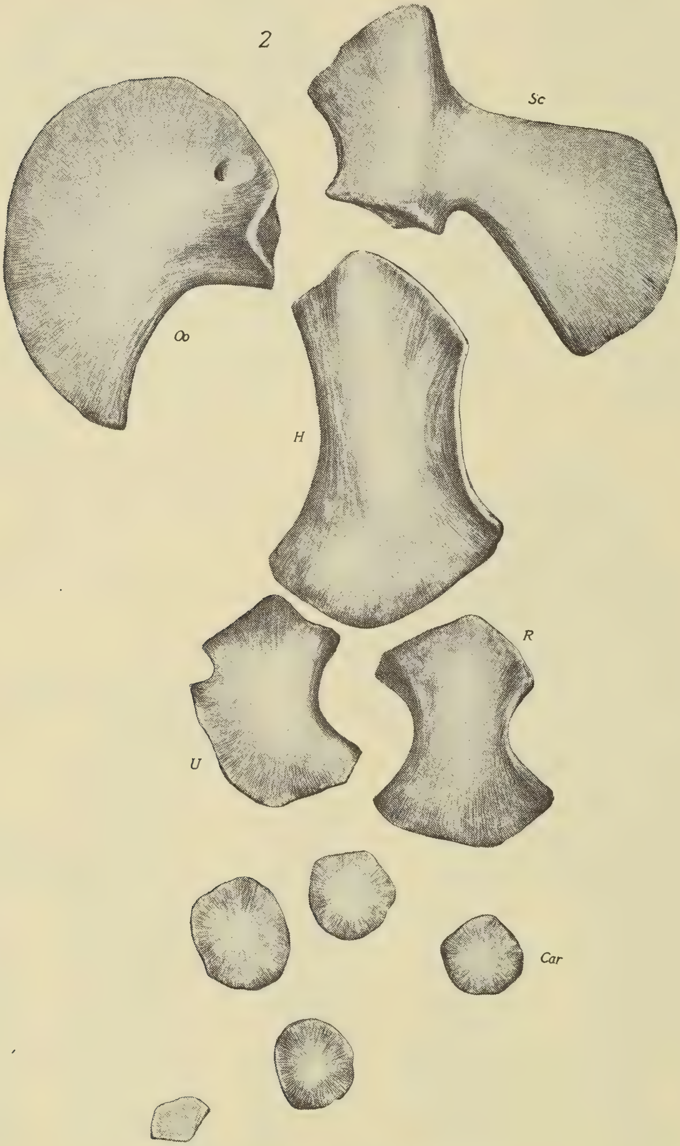
FIG. 1. *Cymbospondylus* (?) *natans*, n. sp. Vertebrae from middle region of caudal fin no. 10624, $\times\frac{1}{3}$.

FIGS. 2*a* and 2*b*. *Cymbospondylus petrinus* Leidy, anterior caudal centrum, no. 8120, $\times\frac{4}{9}$. 2*a*, lateral view; 2*b*, inferior view.

FIGS. 3–7. *Cymbospondylus petrinus* Leidy. Ribs, no. 9950, $\times\frac{3}{10}$.
3, Anterior cervical rib; 4, Posterior cervical rib; 5, Anterior dorsal rib; 6, Middle dorsal rib; 7, Caudal rib.

FIG. 8. *Cymbospondylus petrinus* Leidy. Abdominal ribs, no. 9154, about $\frac{1}{6}$ of natural size.





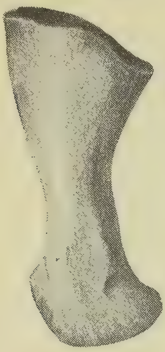
Cymbospondylus petrinus Leidy

Anterior limb and arch, $\times\frac{15}{100}$

From the Middle Triassic of West Humboldt Range, Nevada

FIG. 1. No. 9154. *Cl*, right clavicle.

FIG. 2. No. 9950. Left side: *Sc*, scapula; *Co*, coracoid; *H*, humerus; *R*, radius; *U*, ulna; *Car*, carpals.



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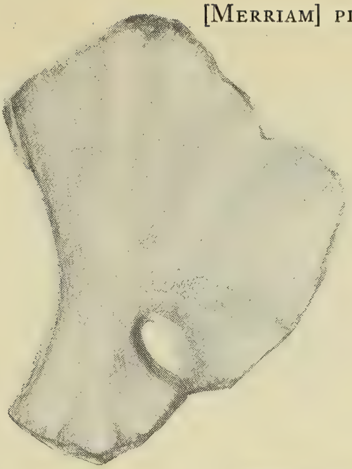

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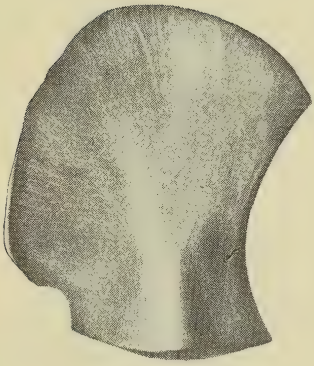

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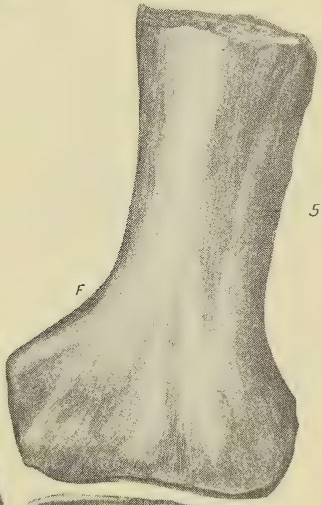
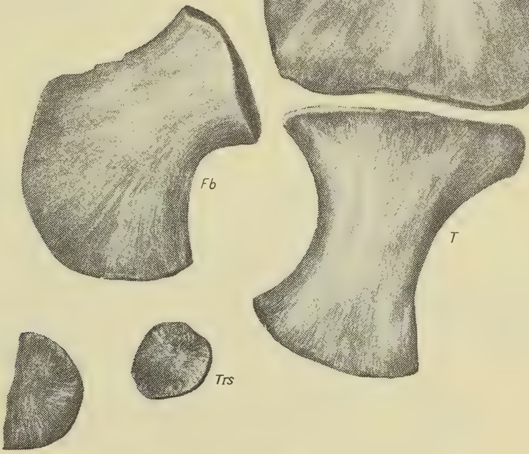
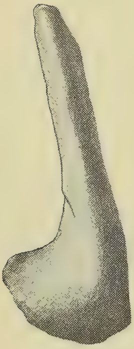






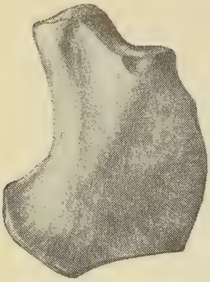
4

Cymbospondylus petrinus Leidy

Posterior limb and arch elements, no. 9947. From the Middle Triassic of West Humboldt Range, Nevada

All figures two-ninths of natural size

FIG. 1. Right ? ilium, posterior side.
FIG. 2. Left ? pubis, superior side.
FIG. 3. Left ? ischium, superior side.
FIG. 4. Right ? ilium, inner side.
FIG. 5. Left ? posterior limb. *F*, femur; *T*, tibia; *Fb*, fibula; *Trs*, tarsals.



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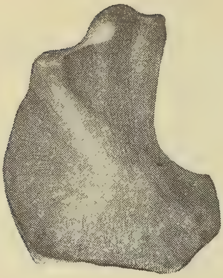
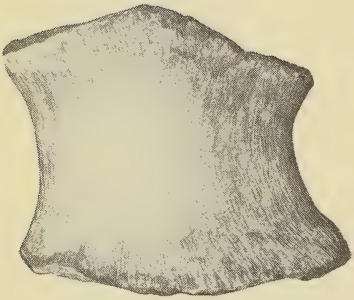


1b



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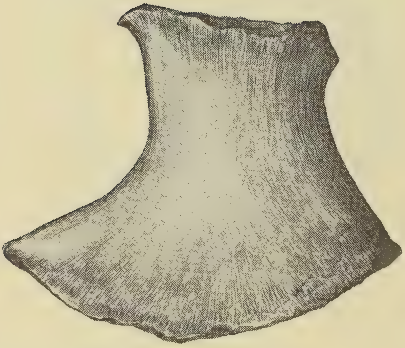

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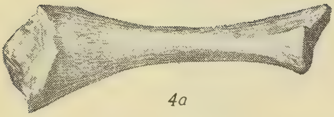

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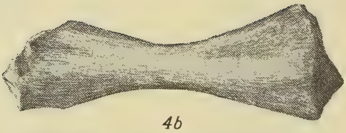

4b

FIGS. 1*a* and 1*b*. *Cymbospondylus* (*?*) *natans*, n. sp. Right humerus, no. 9873, $\times\frac{2}{3}$. From the Middle Triassic, West Humboldt Range, Nevada.

1*a*, superior side; 1*b*, inferior side.

FIG. 2. *Cymbospondylus nevadanus*, n. sp. Tibia?, no. 10620, $\times\frac{3}{10}$. From the Middle Triassic, New Pass Range, Nevada.

FIG. 3. *Cymbospondylus nevadanus*, n. sp. Fibula?, no. 10620, $\times\frac{3}{10}$. From the Middle Triassic, New Pass Range, Nevada.

FIGS. 4*a* and 4*b*. *Cymbospondylus nevadanus*, n. sp. Two views of a caudal rib, no. 10620, $\times\frac{3}{10}$. From the Middle Triassic, New Pass Range, Nevada.

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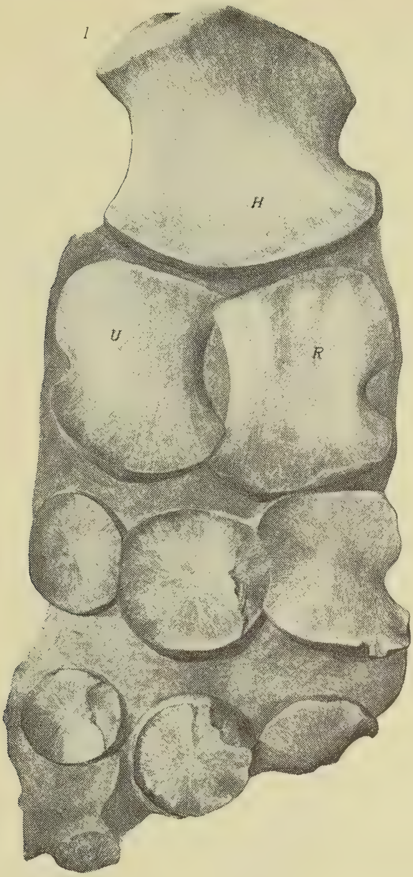

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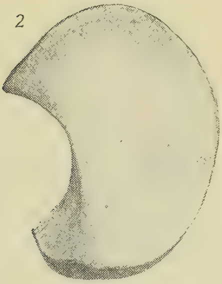

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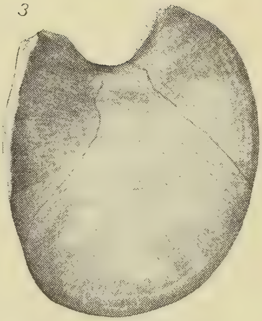

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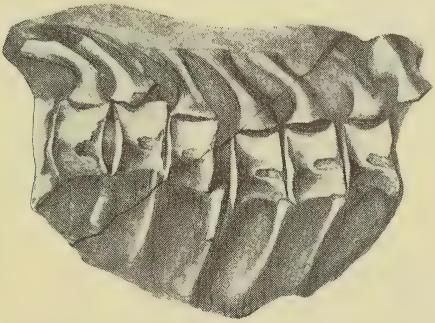


All specimens from the Upper Triassic of Shasta County, California

FIG. 1. *Delphinosaurus perrini* Merriam. Right anterior limb, no. 9082, $\times\frac{1}{2}$. *H*, humerus; *R*, radius; *U*, ulna.

FIG. 2. *Delphinosaurus perrini* Merriam. Left? scapula, no. 9082, $\times\frac{1}{2}$.

FIG. 3. *Delphinosaurus perrini* Merriam. Right coracoid, no. 9082, $\times\frac{1}{2}$.

FIG. 4. *Toretocnemus californicus* Merriam. Anterior caudal vertebrae, no. 8100, $\times\frac{2}{3}$.

EXPLANATION OF PLATE 15

All specimens from the Upper Triassic of Shasta County, California

Fig. 1*a*–1*b*. *Shastasaurus osmonti* Merriam. No. 9076, $\times\frac{2}{9}$. Anterior distal angle of humerus, posterior distal angle of ulna, and posterior side of radiale, restored from elements of right limb of this specimen.

1*a*. Superior side of left anterior limb.

H, humerus; *R*, radius; *U*, ulna; *Rl*, radiale.

1*b*. Proximal end of humerus shown in fig. 1*a*.

Figs. 2*a* and 2*b*. *Shastasaurus careyi* (?) Merriam. No. 9614, $\times\frac{2}{9}$.

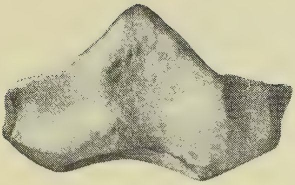
2*a*. Superior side of right anterior limb.

H, humerus; *R*, radius.

2*b*. Proximal end of humerus shown in fig. 2*a*.

Fig. 3. *Shastasaurus osmonti* Merriam. Marginal view of carpal or phalangeal element, no. 9081, $\times\frac{2}{9}$.

Fig. 4. *Shastasaurus osmonti* Merriam. Elements of a transverse row of ossicles in the mesopodial or metapodial region of the anterior limb, showing reduction of the posterior element, no. 9081, $\times\frac{2}{9}$.



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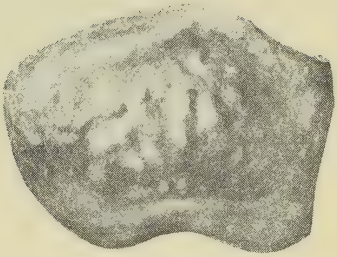

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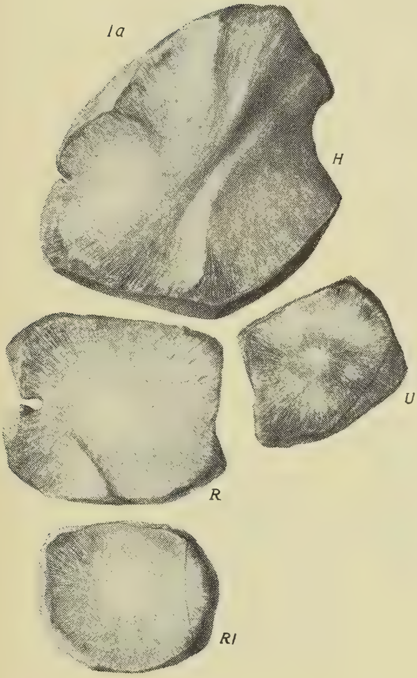

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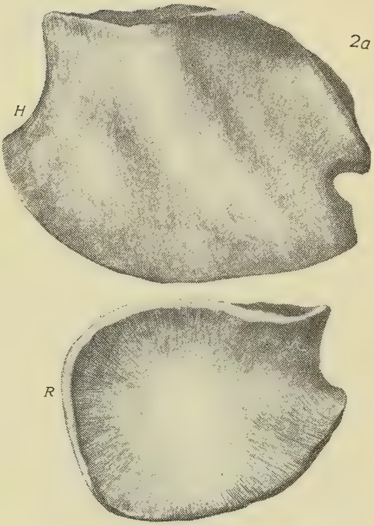

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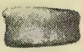

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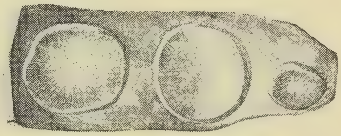

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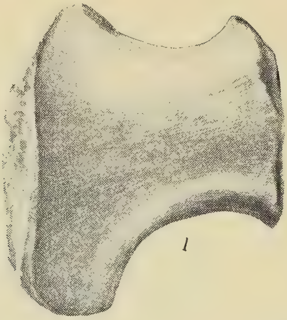
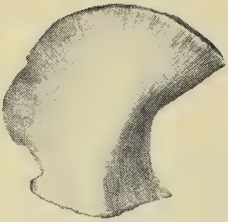
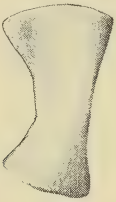
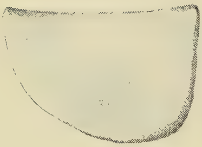
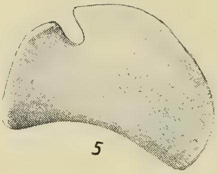
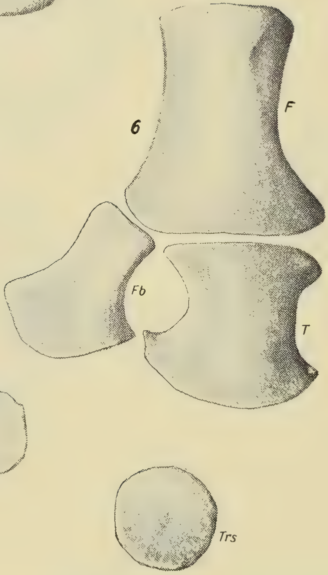










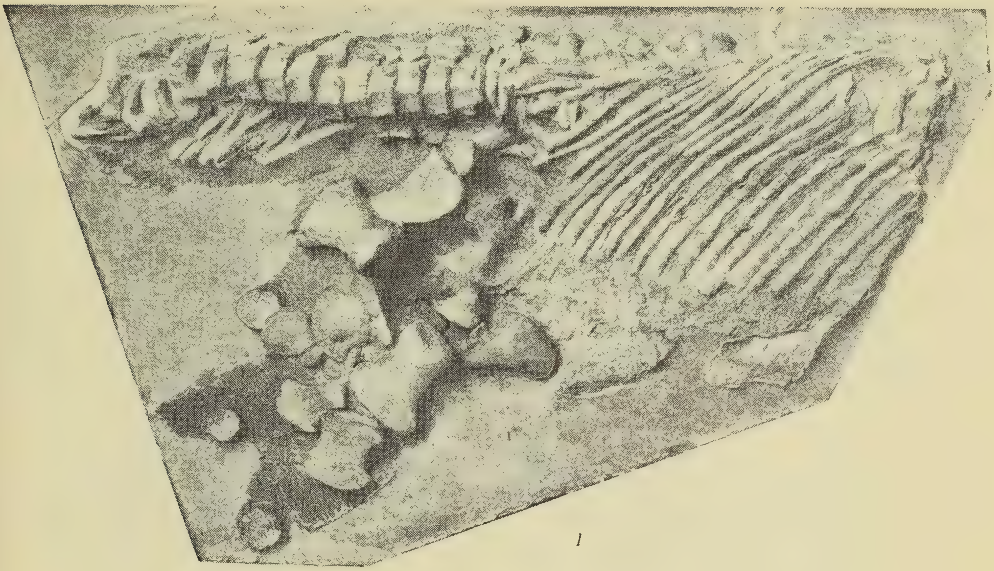


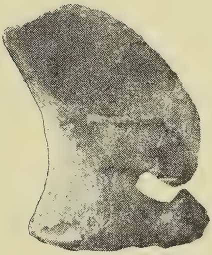
Shastasaurus osmonti Merriam

From the Upper Triassic of Shasta County, California

All figures two-ninths of natural size

Fig. 1. Superior side of right coracoid, no. 9076.
Fig. 2. Superior or inner side of right scapula, no. 9076.
Fig. 3. Ischium, no. 9608.
Fig. 4. Ilium, no. 9608.
Fig. 5. Pubis, no. 9608.
Fig. 6. Posterior limb, no. 9608.
F, femur; *T*, tibia; *Fb*, fibula; *Trs*, tarsals.





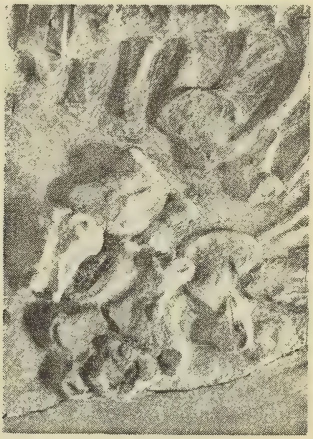
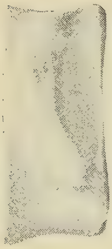
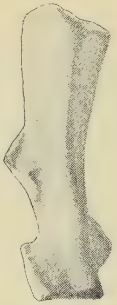


FIG. 1. *Shastasaurus osmonti* Merriam. Posterior dorsal, pelvic and anterior caudal regions, with elements of posterior arch and limbs, no. 9608, about $\frac{1}{10}$ of natural size.

FIG. 2. *Delphinosaurus perrini* Merriam. Elements of posterior arch and limbs, no. 9119, $\times\frac{1}{5}$.

FIG. 3. *Shastasaurus pacificus* Merriam. Pubis of type specimen, about $\frac{1}{5}$ of natural size.





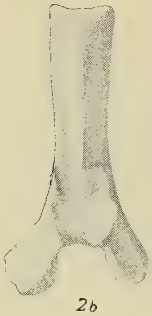
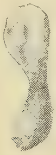
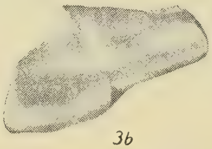
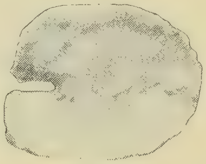


FIG. 1. *Shastasaurus altispinus* Merriam. Middle dorsal centrum, no. 9083.

FIGS. 2*a* and 2*b*. *Shastasaurus altispinus* Merriam. Neural arch of dorsal vertebra, no. 9083. 2*a*, lateral view; 2*b*, anterior view.



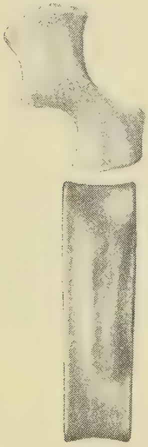


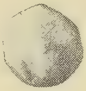


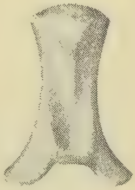
FIGS. 3*a* and 3*b*. *Shastasaurus altispinus* Merriam. Head of a right dorsal rib, no. 9083.

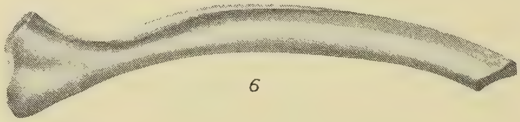
3*a*, articular face; 3*b*, posterior side.

FIG. 4. *Shastasaurus altispinus* Merriam. Element from podial region, no. 9083.









FIGS. 5*a*, 5*b*, and 5*c*. *Shastasaurus careyi* (?) Merriam. Middle dorsal vertebra, no. 9614.

5*a*, lateral view of vertebra; 5*b*, top of neural spine; 5*c*, anterior view of neural arch.

FIG. 6. *Shastasaurus careyi* (?) Merriam. Posterior view of a dorsal rib, no. 9614.

All specimens from the Upper Triassic of Shasta County, California

All figures three-tenths of natural size

THE SKULL AND DENTITION OF A PRIMITIVE ICHTHYOSAURIAN FROM THE MIDDLE TRIASSIC

CONTENTS

Introduction 393
Diagnostic characters 394
Dentition 394
Skull 397
Affinities 399

Introduction

The material described in the following paper comprises two specimens which were obtained in the Middle Triassic limestones of West Humboldt Range, Nevada. One of these (no. 9924), showing a portion of the dentition with parts of the lower jaw, was figured and described for inclusion in a recent paper on Triassic Ichthyosauria,[1] but was finally withdrawn, as its systematic position did not seem clearly determined. A second specimen (no. 9853), which has since been exposed for study, shows the middle portion of a skull, with a dentition similar to that of no. 9924.

The two specimens available, together with a large number of other Triassic ichthyosaurian forms, were discovered in 1895 by the expedition to West Humboldt Range. The work of this party was made possible through the generosity of Miss Annie M. Alexander, who was herself the discoverer of the type specimen.

Although the relationships of the form represented by these specimens are not entirely clear, it has seemed best to publish such information as is available, in the hope that this material may assist in the interpretation of some of the fragmentary saurian remains obtained elsewhere in Middle Triassic formations. The known material representing some of the older marine Triassic

University of California Publications, Bulletin of the Department of Geology, vol. 5, no. 24, pp. 381–390, pl. 40, January 21, 1910.

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[1] Merriam, J. C., Triassic Ichthyosauria, Mem. Univ. Calif., vol. 1, no. 1.

saurians has thus far been very scanty, and the specimens are widely scattered geographically. Only through the publication of illustrations and detailed descriptions of these widely scattered fragments, as they become available, will it be possible to arrive at an understanding of the relationships of the forms which they represent.

DIAGNOSTIC CHARACTERS

PHALARODON FRAASI,[2] n. gen. and sp.

Plate 40

Type specimen, no. 9853, Univ. Calif. Col. Vert. Palae., from the Middle Triassic of south fork of American Cañon, West Humboldt Range, Nevada. Cotype, no. 9924, Univ. Calif. Col. Vert. Palae., from the Middle Triassic of Fisher Cañon, West Humboldt Range, Nevada.

Skull of ichthyosaurian type. Orbits moderately large, superior nares situated a short distance anterior to the orbits. Frontals exposed superiorly almost as far forward as the posterior end of the superior narial openings. Nasals apparently not extending far behind the anterior borders of the orbits, and extending forward only a short distance in advance of the superior narial openings. Angular element of mandible not exposed anterior to the middle of the orbit.

Dentition differentiated; posterior teeth laterally-compressed, low-crowned; most anterior teeth known relatively small, high-conical, nearly circular in cross-section. Teeth inserted in pits which may be situated at the bottom of a shallow groove. Roots showing coarse longitudinal folds, with little or no cement covering.

DENTITION

The first specimen to be obtained (no. 9924) consisted of portions of two lower jaws; and a part of the skull, probably representing the maxillary region, containing two nearly parallel rows of teeth quite similar to those of the lower jaws (pl. 40, fig. 2). Very little of the skeletal structure could be determined as the bones were very fragmentary. The elements of the dentition were well preserved.

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[2] *φάλαρα*, a boss used to adorn head-gear of horses; *ὀδούς*, a tooth. The species is named in honor of Professor Eberhard Fraas, whose contributions to our knowledge of the Ichthyosauria of Europe have been greatly appreciated by the writer in his comparative studies of this group.

The teeth situated on the mandibular elements of specimen 9924 (fig. 1) are of a thick, low-crowned type. They are separated from each other by bony partitions, and appear to be in completely enclosed pits. There is no evidence of the presence of cement surrounding them. Only the thinnest possible cement layer could have been present, as the enclosing bony tissue of the dentary surrounds the roots very closely. The roots are much compressed laterally, and the walls show strong vertical folds. The teeth vary greatly in size and form according to their position in the jaw. The crowns of the most posterior teeth are very low and are considerably compressed laterally. The summits of the crowns are quite abruptly rounded. The most anterior mandibular tooth is hardly more than one-quarter the size of the next to the last one in the series. Its crown is almost round in cross-section, and is more slender and more acute than those of the posterior teeth. Several of the middle teeth represented in figure one have been truncated by wear, but the crowns seem to present transition forms ranging between the quite different types at the two ends of the series. In nearly all of the teeth there is a distinctly constricted neck region at the base of the crown.

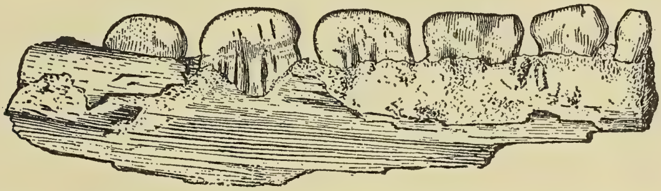

Fig. 1. *Phalarodon fraasi.* Inferior dentition. No. 9924, natural size.

In the superior dentition, one row of teeth contains only a single complete crown, the most posterior one (pl. 40, fig. 2). The crown of this tooth is gently domed, and is compressed laterally. The bases of several crowns anterior to the complete tooth in this row show a rapid decrease in the size of the teeth anteriorly, with a change in the form of the crowns from a laterally flattened cross-section in the posterior ones to a nearly circular section in the most anterior one. In the other superior row, the few imperfectly represented tooth crowns are of the smaller form with nearly circular cross-section, corresponding to the anterior crowns of the superior series described above.

The dentition of specimen 9853 represents four posterior teeth in the upper, and four in the lower jaws (fig. 2). The most posterior tooth present on the maxillary is situated only a short distance in front of the anterior border of the orbit.

The four teeth on the mandible are of nearly the same size. The crowns are low, laterally-compressed domes, on which the antero-posterior diameter considerably exceeds the height of the crown from the base of the enamel to the summit. The summits of the crowns may show distinct radial furrows. The heavy, laterally-compressed roots show a marked infolded or furrowed structure of the lateral walls. The four teeth are rather closely set in the jaw, but seem to be in pits.

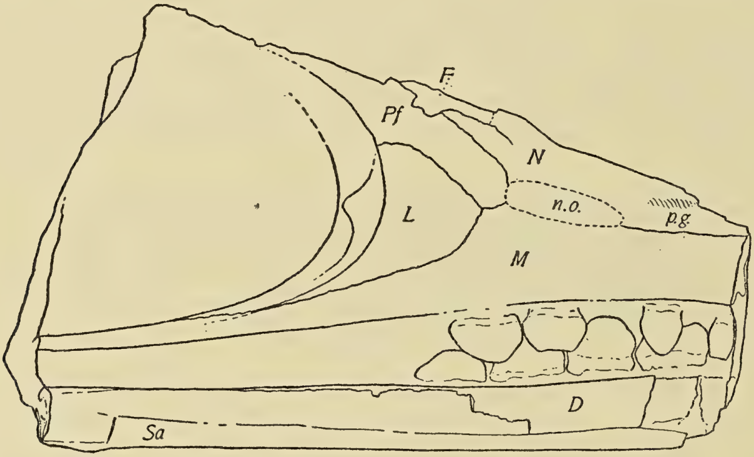

Fig. 2. *Phalarodon fraasi.* Skull and dentition. No. 9853, natural size. *D*, dentary *Sa*, surangular; *M*, maxillary; *L*, lachrymal; *Pf*, prefrontal; *F*, frontal; *N*, nasal; *n.o.*, narial opening; *p.g.*, groove for reception of posterior end of premaxillary.

The teeth of the upper jaw are less closely set than those on the dentary, and other teeth may originally have been present in some of the interspaces. The most posterior tooth resembles the two opposing teeth of the lower series. The second tooth from the back of the series is considerably shorter anteroposteriorly than the last, but retains approximately the same transverse diameter. The anterior pair of teeth are still shorter anteroposteriorly. In the most anterior tooth the cross-section shows only a slight lateral compression. The crowns of the anterior teeth have approximately the same height as the posterior one, but have the form of simple cones, rather than of laterally compressed domes. In the teeth of both jaws the crowns are swollen just beyond the base, but this feature is particularly noticeable in the anterior teeth of the upper jaw, in which the bases of the crowns are much larger than the roots. The enamel of several of the larger teeth shows a tendency to develop radial wrinkles. On the anterior pair of teeth in the upper jaw the enamel is practically smooth. As nearly as can be determined, the anterior upper tooth is set in a shallow pit at the bottom of a shallow, longitudinal groove.

SKULL

The general form of that portion of the skull preserved in specimen 9853 is in many respects closely similar to that in the Ichthyosauria. Anterior to the middle region of the orbits the head narrows gradually to the most anterior point on this specimen (fig. 3). Judging from the form of the skull as shown here, the rostrum was rather slender and pointed, though it may have been shorter than in the typical ichthyosaurs. The skull resembles the ichthyosaurian type in the moderately large orbits and in the position of the superior nares.

The portion of the lower jaw present (fig. 2) shows almost the same vertical diameter for its entire length, and tends to be somewhat narrower vertically below the orbit than in most of the typical ichthyosaurs. Portions of the dentary, surangular, splenial, and probably the angular elements are represented. A portion of the *dentary* is broken away on each side of the skull, but the posterior end seems originally to have extended back about to the middle of the orbit. The alveolar margin of the dentary is wide, the teeth being set a considerable distance in from the outer margin. The *surangular* extends forward to the anterior end of this specimen, and reaches a point anterior to the superior nares. The heavy *splenials* extend the whole length of the skull fragment and reach down to the lower border of the ramus. They are very thin behind the middle of the orbits, but gradually thicken until their diameter immediately anterior to the orbits is several times that opposite the middle of the orbits. The *angular* seems to be represented by a small splint bone situated between the surangular and the splenial just behind the middle of the orbit.

The frontal region is unfortunately only imperfectly preserved, considerable portions of all of the elements represented having disappeared before the specimen was discovered. The *frontals* extend back to a point a little behind the middle of the orbits, where the specimen is broken off posteriorly. The anterior ends of the frontals extend forward almost to the posterior ends of the superior narial openings. Along the superior side of the skull a prominent median ridge is developed at the point of union of the frontals.

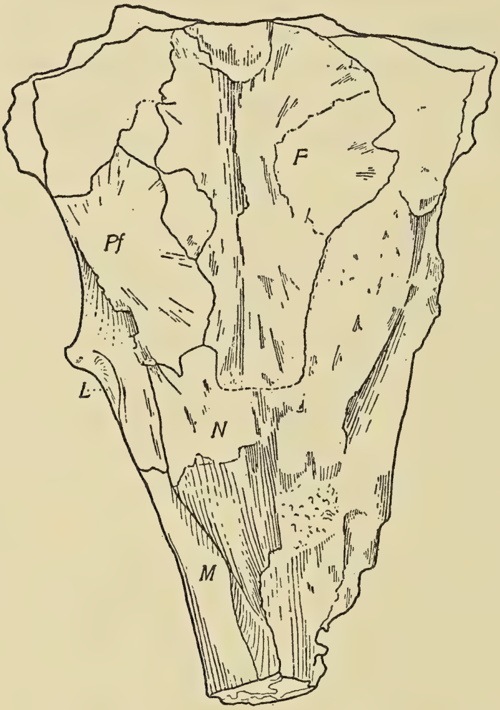

FIG. 3. *Phalarodon fraasi.* Superior aspect of skull. No. 9853, natural size. *F*, frontal *Pf*, prefrontal; *L*, lachrymal; *N*, nasal; *M*, maxillary.

The *prefrontals* are large and extend well in toward the median line of the skull. The centers of radiation of the structure lines of the prefrontals are situated a little behind the anterior borders of the orbits. The anterior ends of the prefrontals extend forward to the posterior ends of the narial openings.

The *lachrymals* are large and form the greater part of the anterior borders of the orbits. The lower end of each lachrymal extends back as a slender splint along the maxillary. The limits of the upper posterior border are not distinctly shown, but seem nearly to reach the superior margin of the orbit. The anterior end of the lachrymal extends very near to the posterior end of the superior narial opening. Almost exactly opposite the middle height of the anterior border of the orbit the lateral portion of the lachrymal is extended outward as a prominent, triangular knob.

The *superior narial opening* is evidently represented on one side of the specimen by a very distinct depression occupying almost exactly the same position in the facial region as the narial opening of the ichthyosaurs. The *nasal* elements border the narial openings above, and extend forward to the anterior end of this specimen, where the terminations are exceedingly slender, indicating that the anterior end was only a few millimeters in front of this point. The nasal bones extend behind the narial openings for a short distance, but appear not to reach back as far as in other ichthyosaurs.

The form of the nasals and frontals seems in this specimen to be quite different from that in the typical ichthyosaurians. The structure does not, however, correspond to that in the Thalattosauria, as the premaxillaries do not seem to form the principal portion of the bar between the superior narial openings. It is, indeed, not probable that the posterior ends of the premaxillaries reached backward between the narial openings.

The *maxillaries* are formed much as in the ichthyosaurs. The premaxillaries appear to be unrepresented. A rather sharply marked groove extending forward across the lateral border of the nasal from the anterior end of the superior narial opening on one side of the skull was probably occupied by the posterior end of a *premaxillary* having much the same form as in some of the ichthyosaurs.

Affinities

The skull of *Phalarodon* resembles that in the Ichthyosauria in its general form. It differs from the typical ichthyosaurs in the form of the frontals and nasals, and in the characters of the dentition. The exposed area of the frontals is much larger than in the typical ichthyosaurs, while the nasals seem to be much smaller than in any form thus far described. Not only have the nasals apparently not extended backward over a large part of the frontal region as in *Ichthyosaurus* and *Cymbospondylus*, but their extension anterior to the narial openings is also much shorter. There seems to be good reason for considering that the premaxillaries were separated posteriorly by the nasals as in the ichthyosaurs and proganosaurs. The lower jaw differs from that of most ichthyosaurs in the shortness of the lateral exposure of the angular element, but in this respect resembles the American Upper Triassic genus *Merriamia*. In the Italian *Mixosaurus* the angular also shows a relatively small lateral exposure.

The dentition most closely resembles that of *Mixosaurus*(?) *atavus* (Quenstedt) as described by Fraas.[3] The specimens available for examination by Fraas showed unfortunately a very few teeth, but careful observations have indicated that, as in the American *Phalarodon*, the dentition was differentiated; while the roots were coarsely folded, were set in partly or entirely separated alveoli, and possessed little or no cement covering.

The amount of differentiation in the European *M.*(?) *atavus* is unfortunately not clearly shown. It is, however, noted that the most posterior teeth have low, domed, laterally-compressed crowns, while the crowns of the teeth immediately anterior are more slender and less flattened laterally.

The dental characters of *M.*(?) *atavus* are so close to those of *Phalarodon* as to suggest very strongly the generic identity of the two. On the other hand the dentition of both forms appears to differ considerably from that of the Italian *Mixosaurus* as described by Repossi.[4] As has been previously suggested by the writer[5] the vertebrae of the *M.*(?) *atavus* forms seem to differ in some particulars from those of the typical *Mixosaurus*. It appears reasonable to give the *M.*(?) *atavus* forms a tentative position in the genus *Phalarodon* until further evidence can be obtained regarding the structure of both the American and the European material.

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[3] Fraas, E., Ichthyosaurier der Süddeutschen Trias- und Jura-Ablagerungen, 1891, S. 38, and Taf. 3, fig. 2 and 3.

[4] Repossi, E., Mixosauro degli strati Triasici di Besano in Lombardia. Atti della Soc. Ital. di Sc. Nat., vol. 41, tav. 8.

[5] Merriam, J. C., Am. Jour. Sc., vol. 19, p. 30, Jan., 1905.

In general skull characters *Phalarodon* seems to represent a member of the Ichthyosauridae more primitive than any form heretofore described. The relatively large exposed area of the frontals, and the relatively small nasals, approach more nearly the form and the relative size of these elements as seen in the early Reptilia generally, than we find them in later ichthyosaurs, or even in the Middle Triassic *Cymbospondylus*. The maxillaries seem also to be comparatively large. It is hardly possible to state definitely whether or not the dentition is primitive, as primitiveness in the sense of closer correspondence to the dentition of the ancestor might possibly be expressed in any one of several tooth forms. The general occurrence of a thecodont tooth insertion in early ichthyosaurs suggests that *Phalarodon* is probably not less primitive than the other forms. As to whether the ancestral ichthyosaur possessed a highly differentiated dentition is somewhat doubtful, but the differentiation of the dentition in the European *Mixosaurus*, in *Phalarodon*(*?*) *atavus*, and in the American *Phalarodon* suggests that differentiation may be a primitive character. A reëxamination of the dentition of *Cymbospondylus* has not as yet shown any evidence of marked differentiation.

Issued January 21, 1910

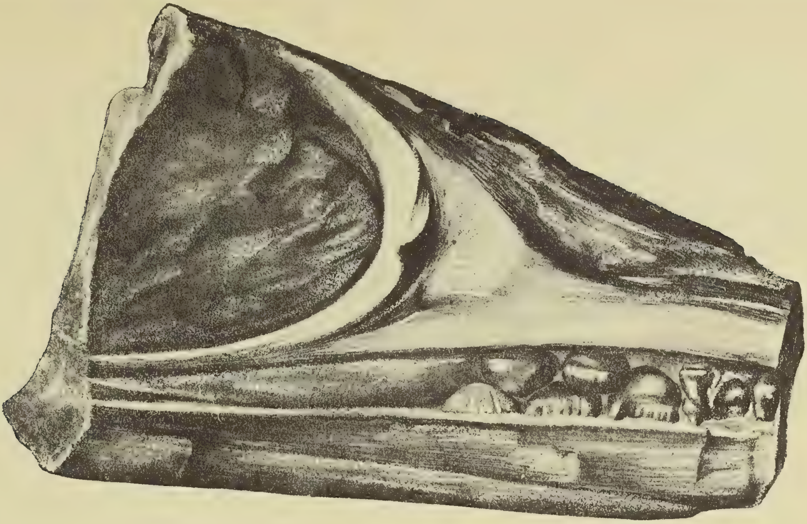

Fig. 1.
Skull and dentition. No. 9853, natural size

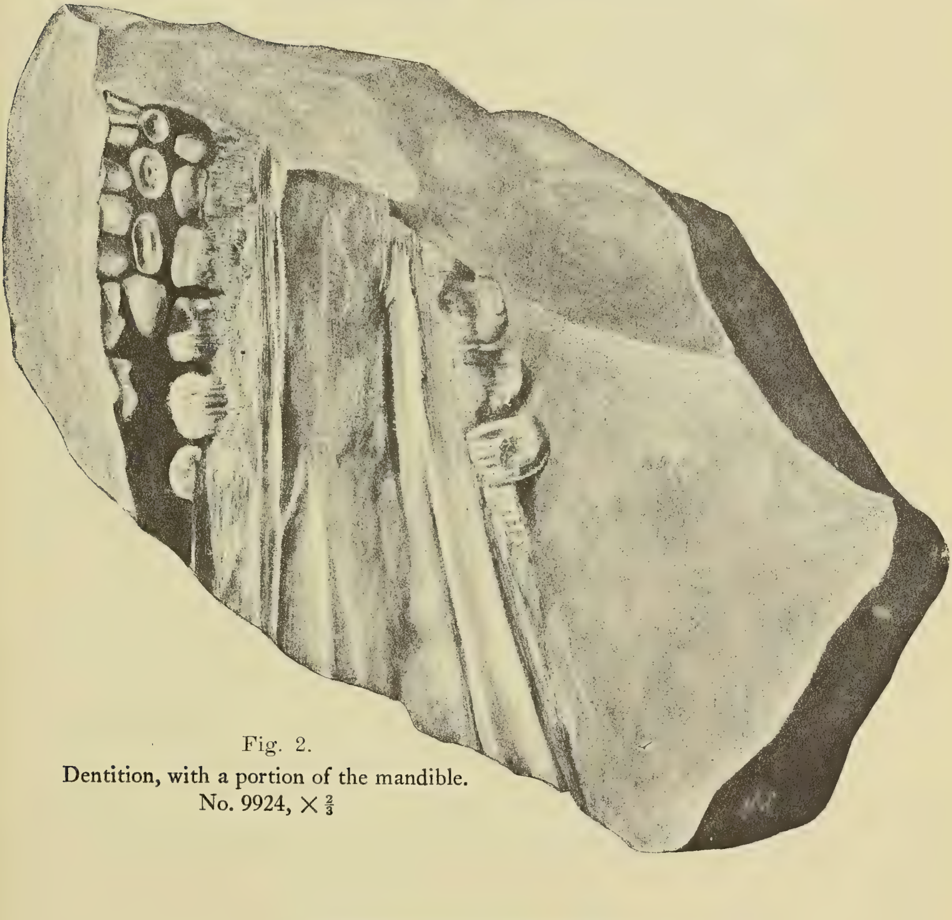

Fig. 2.
Dentition, with a portion of the mandible.
No. 9924, × ⅔

Phalarodon fraasi, n. gen. and sp.
From the Middle Triassic of West Humboldt Range, Nevada

NOTES ON THE RELATIONSHIPS OF THE MARINE SAURIAN FAUNA DESCRIBED FROM THE TRIASSIC OF SPITZBERGEN BY WIMAN

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Introduction

SINCE Nordenskiold's discovery of a number of fragmentary ichthyosaurian specimens in the Triassic of Spitzbergen in 1864[1] the hope has often been expressed that we might know more of the saurian fauna of this interesting region. Though additional material has been obtained from time to time,[2] it was not until recently that any considerable number of specimens was brought together for study.

In 1908 and 1909 important collections were obtained at Spitzbergen by Carl Wiman and Bertil Högbohm, making possible a more satisfactory determination of the nature of the saurian forms represented in this fauna than had previously been possible. The results of a study of the collection by Wiman[3] form a most interesting and important contribution to our knowledge of this group, and materially assist in comparison of the Spitzbergen Triassic with that of the rest of the world.

Occurrence

The ichthyosaurian remains from Spitzbergen are described by Wiman as occurring in two horizons of the middle Trias. The

University of California Publications, *Bulletin of the Department of Geology*, vol. 6, no. 13, pp. 317–327, October 28, 1911.

[1] Hulke, I. W., Bih. till K. Vet. Akad. Handl. Bd. 1, No. 9, 1873.

[2] Yakowlew, N., Verh. d. Russ. Kais. Min. Ges. St. Petersb. Ser. 2, Bd. 40, p. 179. 1902.

[3] Wiman, Carl, Ichthyosaurier aus der Trias Spitzbergens, Bull. Geol. Inst. Upsala, vol. 10, pp. 124–148. 1910.

upper horizon is in the Daonella shales, and contains abundant specimens of the ammonite genus *Ptychites*. The saurian collection from the upper beds comprises *Mixosaurus* (?) *nordenskioldii* (Hulke), and *Pessosaurus polaris* (Hulke).

The lower saurian horizon is about three hundred and fifty feet below the upper beds. Below it is an ammonite fauna including *Ceratites polaris*. At this horizon two saurian forms were found, which are described as *Pessopteryx nisseri*, n. gen. and sp., and *P. minor*. A short distance below the lower horizon a number of large ichthyosaur teeth were found.

Excepting the specimens representing *M.* (?) *nordenskioldii*, all of the material from Spitzbergen unfortunately consists of scattered or isolated bones. The *M.* (?) *nordenskioldii* specimens are much better preserved than the others, and in some cases show considerable connected parts of skeletons.

MIXOSAURUS (?) NORDENSKIOLDII (Hulke)

Both *Mixosaurus* (?) *nordenskioldii* and *Pessosaurus polaris* were first described by Hulke in 1873 under the name of *Ichthyosaurus*. Since that time it has been clear to several writers that they could not remain in that genus, and various suggestions as to their possible relationships have been made by Dames,[4] Yakowlew,[5] and Merriam.[6]

Wiman's studies of *M.* (?) *nordenskioldii* make possible for the first time a fairly satisfactory suggestion as to the affinities of this form. From a study of the excellently preserved material of this species Wiman has been able to show the close similarity of this form to *Mixosaurus cornalianus* from the Besano beds of northern Italy, and also to the imperfectly known *Cymbospondylus* (?) *natans* from the Middle Triassic of the West Humboldt Range in Nevada.

The *skull* of *M.* (?) *nordenskioldii* is known only by a few fragments. Fortunately in many instances these pieces bear teeth, so that some important characteristics of the dentition appear. As was shown by Dames, the *dentition* is thoroughly differentiated. The posterior teeth are low, laterally-compressed domes, the anterior teeth are small, approximately conical, and round in cross-section. The roots are coarsely folded as in the specimens of *M.* (?) *atavus* described by Fraas,[7] from the middle Trias of Germany, and are set in more or less distinctly separated alveoles. The dentition in several specimens, as appears in figure one adapted from Wiman, is very close to that of *Phalarodon*, a Nevada Middle Triassic form recently described[8] by the writer. The teeth of other specimens (fig. 2) are less like *Phalarodon* and more like *Mixosaurus* of the Italian Triassic. It seems not impossible that two types are represented in Wiman's material.

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[4] Dames, W., Sitzb. d. Acad. d. Wiss. Berlin, 1895, p. 1045.

[5] Yakowlew, N., Verh. d. Kais. Russ. Min. Ges. Bd. 40, p. 179. 1902.

[6] Merriam, J. C., Univ. Calif. Publ. Bull. Dept. Geol. vol. 3, pp. 87, 88. 1902.

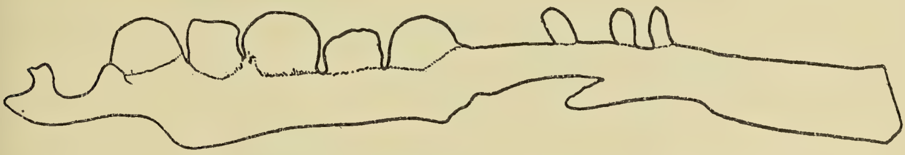

FIG. 1. *Mixosaurus* (?) *nordenskioldii* (Hulke). A portion of the lower jaw with dentition. Natural size. (After Wiman.)

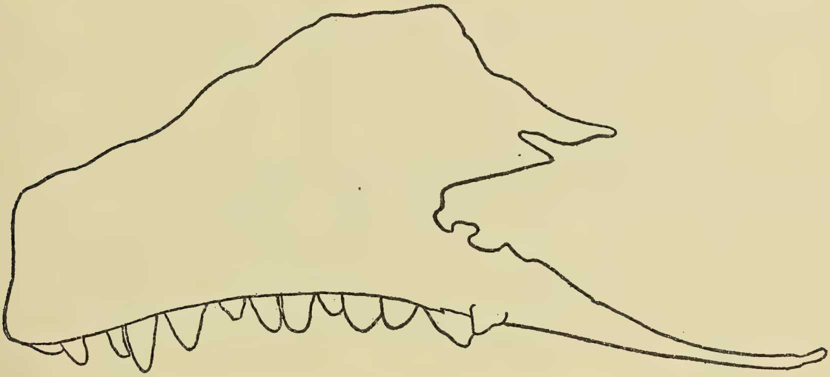

FIG. 2. *Mixosaurus* (?) *nordenskioldii* (Hulke). Upper jaw fragment with dentition. Natural size. (After Wiman.)

One of the most interesting discoveries made by Wiman is the finding of excellent material representing the *limbs* and arches of *M.* (?) *nordenskioldii.* Both anterior and posterior limbs were obtained in such excellent state of preservation that nearly all the essential characters can be determined. In both limbs the epipodial elements are distinctly elongated and separated by a median cleft as in most Triassic ichthyosaurs, and the phalangeal elements generally show the median constriction, which has been considered as representing a rudimentary shaft region.

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[7] Fraas, E., Ichthyosaurier der Süddeutschen Trias- und Jura-Ablagerungen, 1891, p. 38; Taf. 1, figs. 17 and 18, and Taf. 3, figs. 2 and 3.

[8] Univ. Calif. Publ. Bull. Dept. Geol. vol. 5, p. 382. 1910.

The *anterior limb* (fig. 3) is in general much like that of *Mixosaurus cornalianus* of the Italian Triassic. It differs from the Italian specimens thus far described in possessing a sixth digit. The first three segments of the anterior limbs are practically identical with those of *Cymbospondylus* (?) *natans*, a Mixosaurus-like species from the Middle Triassic of Nevada. The *posterior limb* (fig. 4) is almost identical in form with that of *Mixosaurus cornalianus*, even to the duplication of a peculiar arrangement of the proximal carpals found in the Italian species.

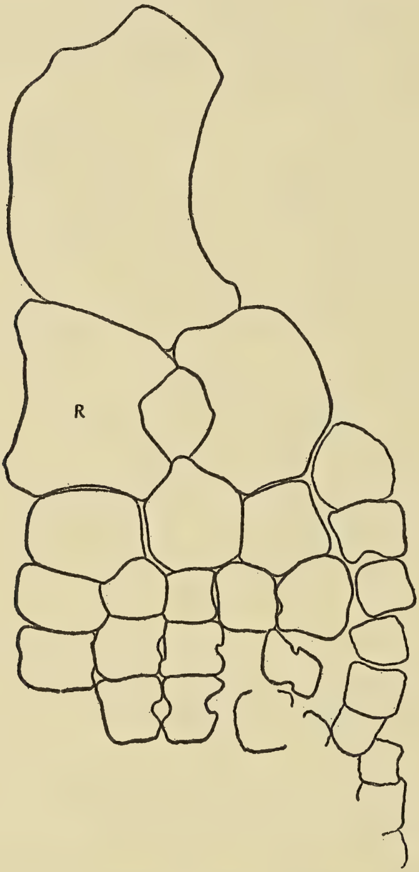

FIG. 3. *Mixosaurus* (?) *nordenskioldii* (Hulke). Anterior limb, × $\frac{2}{3}$. *R*, radius. (After Wiman.)

The *pelvic arch* (fig. 4) is almost identical with that in most specimens of the American *Cymbospondylus*, and differs from that of *Mixosaurus* in the absence of an obturator foramen in the pubis.

The *pectoral arch* is like that of *Mixosaurus* excepting in the form of the interclavicle, which has a remarkably wide triangular form with a distinct reëntrant angle on the anterior side.

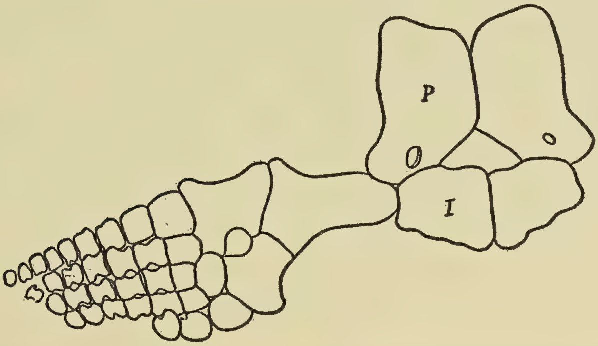

FIG. 4. *Mixosaurus* (?) *nordenskioldii* (Hulke). Pelvic arch and posterior limb, × ½. P, pubis; I, ischium. (After Wiman.)

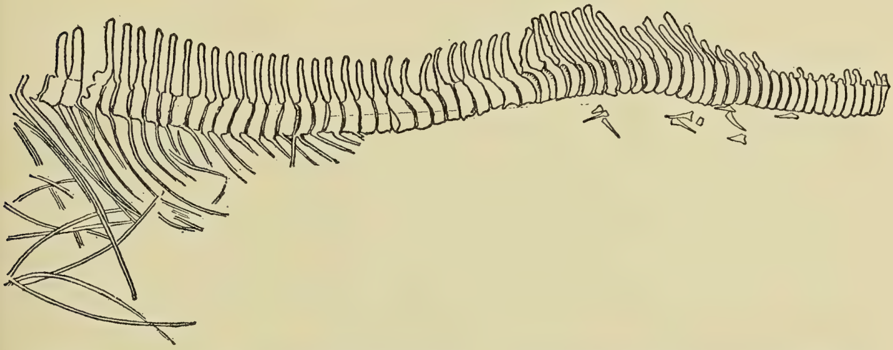

FIG. 5. *Mixosaurus* (?) *nordenskioldii* (Hulke). A portion of the dorsal and caudal series, × ⅕. (After Wiman.)

The complete *vertebral column* is not known, but fortunately considerable numbers of vertebrae, including the posterior dorsal region and a large part of the tail, were found in a continuous series (fig. 5). As in *Mixosaurus cornalianus*, the tail makes a gentle upward curve near the middle and droops slightly at the posterior end. In the Spitzbergen form as represented in the specimen figured by Wiman the upward curve is much nearer the dorsal region than in *M. cornalianus*; in contrast to *Cymbospondylus*, in which the curve is farther back than in the Italian species.

The posterior dorsal and the caudal vertebrae are characterized by very high, slender neural arches. The arches stand nearly erect over the posterior dorsal and anterior caudal regions, but are suddenly turned sharply forward near the middle of the bend in the tail. The centra of the caudal region are considerably increased in both relative and absolute height behind the middle of the bend, and are very noticeably flattened laterally.

In a reconstruction of *Mixosaurus* (?) *nordenskioldii* published by Wiman (fig. 6), the expansion of the caudal fin is represented as widest at a point only a short distance posterior to the pelvic limb. Wiman's reconstruction is apparently based on the proportions of a specimen showing the posterior dorsal and caudal region as reproduced in figure five. In this specimen as figured there is an extraordinarily sudden lengthening of the neural spines immediately behind a break in the specimen, which suggests, as a bare possibility, the loss of a portion of the caudal series at this point. It is also worthy of note that the original position of the pelvis is very difficult to determine, and it may easily have been situated considerably farther forward than the point in the column below which the ilium now rests. A modification in one or both of these particulars might change the relative position of the upper lobe of the caudal fin. It would seem to the writer that a propeller constructed as represented in this form would be far from the most efficient type. It would also represent a distinct deviation from what appears to be the natural line of evolution of the typical ichthyosaur out of a Palaeohatteria-like shore form. In an earlier publication[9] the writer has

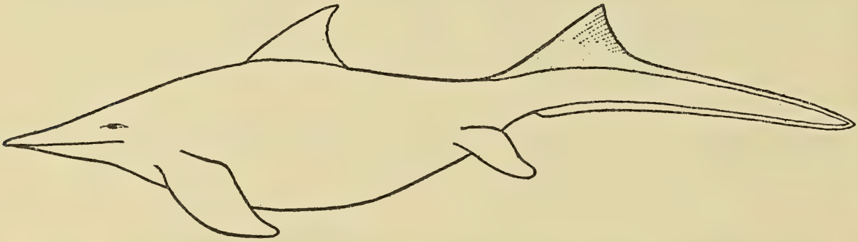

FIG. 6. Restoration of *Mixosaurus* (?) *nordenskioldii* (Hulke). (After Wiman.)

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[9] Merriam, J. C., Triassic Ichthyosauria, Mem. Univ. Calif., vol. 1, p. 40. 1908.

suggested that the probable course of evolution of the ichthyosaurian caudal fin has been through a series of forms in which the tail fin was first distinctly adapted for service as a propeller by increase in height some distance anterior to the tip through elongation of the neural arches. This was possibly accompanied by a slight droop of the extreme posterior region. Through the stages of *Cymbospondylus* (*?*) *natans* and *Mixosaurus cornalianus* a superior lobe developed over the elongated spines. Once developed, this lobe remained and increased in importance. The support of the neural spines came to be unnecessary and their arches were much reduced in the later stages of evolution of the group.

The *rib articulation* is not clearly shown for the whole vertebral series, and is unfortunately not known in the cervical and anterior dorsal regions. Some of the vertebrae bear widely separated diapophyses and parapophyses as in *Toretocnemus* from the West American Triassic. These centra are from the middle or posterior dorsal region.

PESSOSAURUS POLARIS (Hulke)

A number of specimens representing a large saurian from the upper bed are included by Wiman in Hulke's species *Ichthyosaurus polaris*, which is, however, separated as a distinct genus *Pessosaurus*. If the several specimens referred to this genus actually belong together, the only distinguishing character of the group would seem to be in the humerus. The element considered as the femur is like that of *Shastasaurus*. The short humerus is nearly circular in form, and differs from that of *Shastasaurus* in the absence of any trace of a median constriction. In the most specialized forms of *Shastasaurus* the humerus is relatively shorter than in *P. polaris*, but evidence of an original median constriction appears in the anterior and posterior notches. The carpal and phalangeal elements of *Pessosaurus* are apparently round, and evidently lay in a cartilage plate as in *Shastasaurus* and in *Baptanodon*.

PESSOPTERYX

Of the specimens referred to *Pessopteryx* the only remains of the skull consist of jaw fragments, of which the exact position in the skull is not known. The teeth carried by these fragments are numerous, and the hemispherical crowns seem to be set in many rows. They were first thought by Wiman to be pavement teeth of fishes, but against this idea he has rightfully urged that they are numerous, and are the only teeth occurring with the saurian remains in the lower horizon. The presumption is in favor of the view that they represent the same form as some of the saurian bones. As is suggested by Wiman, the dentition represented in these specimens differs from that of ichthyosaurs in the quite uniformly smooth, hemispherical tooth-crowns, and in their arrangement in numerous rows. In one specimen figured, the roots are shown to have infolded walls, as in the Ichthyosauria. It is, however, worth noting that the figured specimen (Wiman, pl. 9, fig. 30) showing the folded root-structure is much larger than any of the others. The specimen shown in Wiman's figure 26, plate 9, which most nearly approaches in size the specimen with a slightly folded root-structure, does not certainly show the arrangement of teeth in several rows. The combination of characters seen in this dentition is quite unlike that of any known member of the Ichthyosauria. Very low, domed tooth-crowns are known in the most posterior teeth of the genus *Phalarodon*,[10] but in this and in other somewhat similar primitive ichthyosaurs the teeth are in a single row, and the low-crowned posterior teeth rapidly change to a sharply conical form in the middle and anterior region of the jaw. In all of the characters mentioned, excepting in the folded roots, the peculiar teeth on most of the specimens figured by Wiman resemble the dentition of the genus *Omphalosaurus* from the Middle Triassic of Nevada.[11]

Omphalosaurus was described from a single specimen representing a skull with a portion of the dentition. A few vertebrae were connected with the skull, and several limb bones were doubtfully associated with it. The structure of the skull was not clearly understood, but it did not seem to correspond to that of any known reptilian family. The inferior dentition consisted of several rows of hemispherical, to low-conical teeth on each dentary. The inferior dentition collectively formed a strongly convex crushing surface, which presumably indicated that the facial region was short. Other specimens which have been obtained at the same horizon as the original one show the dentition better than in the type. In each case the tooth-crowns preserve a nearly unvarying form, and the surface of the tooth-pavement is convex.

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[10] Merriam, J. C., Univ. Calif. Publ. Bull. Dept. Geol. vol. 5, p. 383. 1910.

[11] Merriam, J. C., Univ. Calif. Publ. Bull. Dept. Geol. vol. 5, p. 76. 1906.

Other skeletal remains which have been thought by Wiman to represent the same genus as the jaws bearing hemispherical teeth comprise a number of vertebrae and many elements representing the limbs and arches. The vertebrae are not distinctly different from those of certain Triassic ichthyosaurs. So far as can be determined this may also be true of the vertebrae associated with the type specimen of *Omphalosaurus*. The limb bones referred to *Pessopteryx* are all such as might belong to an ichthyosaur of the type of *Shastasaurus*. Short limb elements of a similar nature were associated with the type specimen of *Omphalosaurus*, but were not described, as there seemed a possibility that the association was purely accidental. While one would not be justified in holding that all of the limb elements referred by Wiman to *Pessopteryx* actually represent the same genus as the jaws with button-like teeth, there seems a reasonable possibility that some of them belong to that group.

It seems to the writer probable that some, if not all, of the Spitzbergen forms with button-like teeth arranged in several rows are referable to a genus closely allied to *Omphalosaurus*. It would not be surprising if there were associated with these a number of specimens of ichthyosaurs of the *Phalarodon* type. This is at any rate precisely the association found in the Middle Triassic of Nevada.

Faunal Relationships

The saurian forms represented in the Triassic of Spitzbergen show a noticeable similarity to those of the Triassic of western North America and of central and southern Europe. *Mixosaurus* (?) *nordenskioldii* of Spitzbergen is apparently close to *Mixosaurus cornalianus* of Italy, and seems also nearly identical, so far as known, with *M.* (?) *natans* of the Middle Triassic of Nevada. Some of the Spitzbergen forms referred by Wiman to *Mixosaurus* show a general similarity of the dentition to that of *M.* (?) *atavus* of central Europe, as also to that of *Phalarodon* of the Middle Triassic of Nevada. The resemblance of some of the Spitzbergen specimens included in *Pessopteryx* to *Omphalosaurus* of the Nevada Middle Triassic is such as to suggest close relationship, if not generic identity of the two forms.

The stage of evolution of the Spitzbergen fauna is not easily estimated with the material available. As nearly as can be determined *M.* (?) *nordenskioldii* is near the stage of evolution of *M.*

cornalianus and *M.* (?) *natans.* It may be slightly less advanced than *Cymbospondylus*, but difference in size of the individuals compared may prevent a satisfactory determination of the relative stages of advance.

The forms of the *Pessosaurus polaris* type in the Spitzbergen fauna suggest the stage of evolution seen in *Shastasaurus* of the Californian Upper Triassic. It should, however, be stated that fragmentary specimens of a somewhat similar nature have been seen in the Middle Triassic of Nevada. There is as yet insufficient evidence to permit an interpretation of this Nevada material. It is not impossible that specialized short-limbed forms were beginning to appear in the Nevada Middle Triassic, though not yet an important or dominant type as in the Upper Triassic.

On the whole, such evidence as is available suggests that the saurian fauna of the Spitzbergen Triassic is not far removed in time from the *Cymbospondylus* fauna of the Middle Triassic of Nevada, and that it is also near the age of the *Mixosaurus* fauna of the Besano beds of Italy. It may also be assumed that at the period in which these faunas flourished there was free communication between the sea areas of the Spitzbergen, Nevada, and north Italian regions.

Transmitted July 28, 1911

NOTES ON THE DENTITION OF OMPHALOSAURUS

Introduction

In the saurian collections which have been obtained in the marine Middle Triassic of Nevada during the last ten years a number of specimens have appeared which represent a form apparently differing from all known reptilian types. A portion of a skull representing this group was described by Merriam[1] in 1906 as the type of the genus *Omphalosaurus.* In the absence of complete material it was not possible to determine definitely the relationships of the genus, and it may be placed tentatively in a distinct order, the Omphalosauria. So far as known the animal is a short-headed form, presumably of the synapsidan type. The structure of the palate and the mandible are not unlike that in the plesiosaurs, while other characteristics point toward the rhynchocephalian type. One of the remarkable features of this specimen is found in the nature of the dentition. The dentary elements are set with several rows of teeth, the crowns of which are nearly circular in cross-section, and dome-like in elevation. There are at least three rows of teeth on the dentary, with the presumption that many more rows may have been present. The surface of the dentigerous area of the mandible was evidently strongly convex. The nature of the dentition suggests that of certain fishes, while characters of the skull are unquestionably reptilian.

Since the publication of the original description of this form Wiman[2] has described from Spitzbergen a number of specimens which he refers to the ichthyosaurs, but which are interpreted by Merriam[3] as probably representing omphalosaurians. The specimens obtained by Wiman occurred in beds which are considered as representing the Middle Triassic, and the saurian fauna is in general

By John C. Merriam and Harold C. Bryant. *University of California Publications, Bulletin of the Department of Geology*, vol. 6, no. 14, pp. 329–332, October 28, 1911.

[1] Merriam, J. C., Univ. Calif. Publ. Bull. Dept. Geol., vol. 5, p. 76, 1906.

[2] Wiman, C., Bull. Geol. Inst. Upsala, vol. 10, p. 140, 1910.

[3] Merriam, J. C., Univ. Calif. Publ. Dept. Geol., vol. 6, p. 325, 1911.

quite similar to that of the Middle Triassic of the West Humboldt Range, in which the type specimen of *Omphalosaurus* was found.

EVIDENCE PRESENTED BY NEW MATERIAL

In the material most recently obtained from the Middle Triassic of Nevada there are two closely associated specimens showing a great number of large, bluntly-conical teeth resembling in general the teeth of *Omphalosaurus*. Thus far a study of these specimens has failed to reveal the exact relationships of all of the bony elements exposed. The characters of the dentition are much better shown than in the type specimen of *Omphalosaurus*.

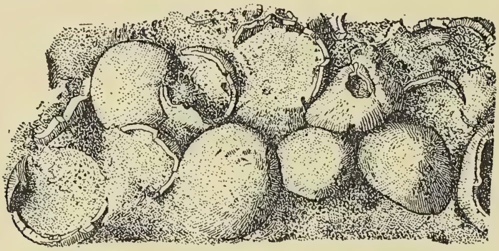

FIG. 1. *Omphalosaurus* (?), sp. A portion of the dentition of the mandible (?). No. 19452, natural size.

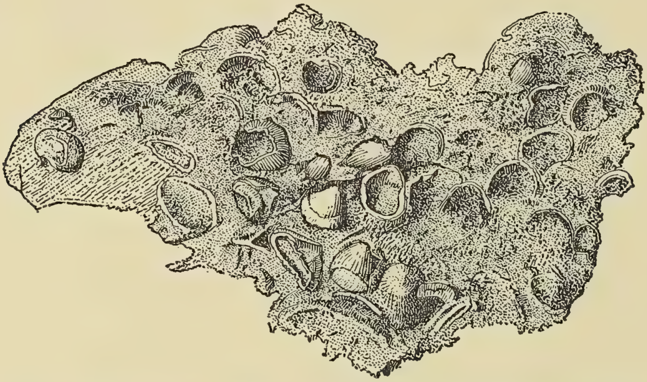

FIG. 2. *Omphalosaurus* (?), sp. Portion of a dentition in which the teeth show a tendency toward a low-conical form. No. 19453, natural size.

One specimen (no. 19452) shows the dentition of a part of what appears to be the dentary. The dentigerous area exposed is a strongly convex surface. The largest and best preserved teeth are situated at the rounded anterior portion. Running posteriorly on each element the teeth decrease in size. The area having the best preserved teeth shows them in irregular rows. There are at least five rows anteriorly, but only three distinguishable at the posterior extremity of the element. This arrangement, however, is not so apparent on the rest of the dentigerous area, where the teeth are broken off or are crushed together. No part of the elements exposed appears to be edentulous, teeth being found out to the margins.

The other specimen (no. 19453) apparently shows several of the bones belonging to the skull, and the cross-section of an element bearing nine or ten teeth similar to those on the type specimen.

As nearly as can be determined on the omphalosaur-like material available the teeth rest in distinct pits. The pits vary from two to six millimeters in depth and from three to fifteen millimeters in greatest diameter. In all cases the depth of the pit is less than the greatest transverse diameter, and is nearly the same as the height of the tooth-crown.

The crowns are quite uniformly dome-shaped, with a nearly circular cross-section. The largest tooth measures fifteen millimeters in greatest transverse diameter. The enamel does not appear to be perceptibly roughened. The short, bluntly-conical roots show no radial folding of the dentine as in the ichthyosaurs.

The dentition described does not closely resemble that of any form known to the writers. The evident reptilian character of the skeletal elements precludes any close relationship to the pyconodont fishes or to the cestracionts. Of the reptilian forms the rhynchosaur *Hyperodapedon* has several rows of depressed conical teeth on the maxillary and palatine. They are, however, quite different in size, and apparently in function, while the skull characters of the two forms are far apart. Whatever the relationships of *Omphalosaurus* may prove to be when the skeleton is better known, the dentition is evidently a peculiarly specialized one, which has been adapted to a diet of which shell-covered mollusca formed an important part.

Transmitted July 11, 1911

MARINE REPTILES

TEN YEARS' PROGRESS IN VERTEBRATE PALEONTOLOGY

During the past ten years important additions to our knowledge of all the great groups of marine reptiles have been made, but in certain of them, as the mosasaurs, which had received especial consideration during the preceding decade, this advance was relatively small.

The contributions which have added most to our knowledge of special groups would seem to the writer to be:

1. The full description and interpretation of the thalattosuchian crocodiles.
2. The additions to our knowledge of the skeletal structure, habits, and relationships of the plesiosaurs.
3. The description and interpretation of the structure of the Triassic, late Jurassic, and Cretaceous ichthyosaurs.
4. The description of a typically marine group of rhynchocephalian or diaptosaurian reptiles.

Of much interest are also the studies of the marine turtles, *Archelon* and *Protostega*, initiated just before the beginning of the past decade; the monographic revision of the marine turtles of America; the discussion of the structure, habits and origin of the mosasaurs; and the description of a new marine reptilian type, the omphalosaurs, which does not as yet seem to find a clearly defined place in our classification scheme of the Reptilia.

Important collections representing marine reptiles have been brought together by many institutions during the past decade, but the value of this material in advancing our knowledge will in many cases not be determined until the completion of studies now in progress. Of the collections which are known to the writer especial importance seems to attach to the splendid plesiosaur and ichthyosaur material from the Oxford Clay which has become the property of the British Museum; the complete plesiosaur speci-

Bulletin of the Geological Society of America, vol. 23, pp. 221–223, June 1, 1912.

mens obtained from Holzmaden by the Royal Museum of Stuttgart; the extraordinary American plesiosaur material acquired by the University of Kansas; the *Baptanodon* specimens, which have been obtained from the American Jurassic by the University of Wyoming, the Carnegie Museum, and the American Museum; the splendid American mosasaur specimens acquired by the American Museum, the University of Chicago, and the Geological Institute of Tübingen; the collections of ichthyosaur material from the Cretaceous of Germany obtained by the University of Munich; the Triassic ichthyosaur collections from Spitzbergen secured by the Geological Institute of Upsala; and the collections of Triassic ichthyosaurian, thallatosaurian, and omphalosaurian remains assembled from California and Nevada by the University of California.

During the past decade the following problems relating to the marine Reptilia have been subjects for general discussion:

1. Adaptation and affinities of the Thalattosuchia—Now known to be typical aquatic forms, but not entirely limited to high seas.

2. Relation of Pasasuchia to true Crocodilia—Pasasuchians separated as a distinct order.

3. Origin of the Mosasauria and habitat of young forms—Views as to derivation from a Varanus-like form of Lower Cretaceous age more fully expressed than previously. General absence of specimens representing young suggests that they possibly lived in fresh water.

4. Relationships of the order Ichthyosauria—Suggestions as to relationship to Rhynchocephalia, to Pasachusia, to Cotylosauria, and to Proganosauria. View that the ichthyosaurs originally had a lateral temporal fenestra seems not supported by evidence of the Middle Triassic forms. No clearly defined theory as to origin of this group has been worked out. Probably an old order near Cotylosauria, and has many points in common with the proganosaurs.

5. The origin and course of evolution of the marine turtles, and particularly the course of evolution of the Recent Dermochelyidæ.—Extremely varied opinions as to origin of the leatherback turtles have been expressed. The questions involved have a very important relation to the problem of origin and evolution of the Testudinata.

Of the numerous lines of investigation in the study of marine reptiles now open to us, the following seem to promise important results:

1. A thorough search in all known marine deposits of Lower Triassic age for ancestral forms of the ichthyosaurs and omphalosaurs.
2. Extensive search for marine reptilian remains in the Middle and Upper Triassic of Europe, coupled with an exhaustive comparative study of the collections of marine Triassic forms in all of the European museums.
3. Exploration of marine Mesozoic formations in Asia, with special reference to obtaining material representing early forms of the Ichthyosauria, Plesiosauria, and Mosasauria.
4. An exhaustive examination of the evidence obtained from a study of the history of marine Reptilia with particular reference to its bearing upon the problem of cause and process in evolution.

In a study of the marine reptiles we are necessarily concerned with many problems relating to the morphology, relationships, geologic range, geographic range, probable habits, and ecological relations of each member of each group. One phase of any problem for any member of a group may well furnish a profitable subject for exhaustive investigation, but the ultimate biological value of all such work depends largely upon the extent to which it assists in an understanding of the processes involved in the evolution of the organic world, and through this means helps to interpret life in the broad sense. Viewed in this light, the marine reptiles, together with the marine mammals, without regard to their position in the scheme of classification, furnish a problem of peculiar interest, which seems to the writer to be one of the large questions still before us for solution. By reason of the peculiar environment in which marine forms of all ages and all quarters of the earth's surface have lived, the problem of their evolution is more sharply defined than in most groups, and therefore perhaps more easily investigated.

The significance of the changes which have taken place in the history of the marine reptiles and mammals has been held by some to be relatively slight in so far as the probability of their throwing light on the problem of cause or mode of evolution is concerned, as the possibilities of change or modification are narrowed in these forms by reason of the peculiar environment. If the influence of selection be considered a factor, it could work only in one direction, if worked at all. To some, natural selection unaided does not seem in any way competent to account for the rapid evolution through numerous stages shown by these reptiles; and the influence of the environment either through the direction of mutations or through directing the mode of use of organs, and therefore possibly the development of the animal, has been considered responsible to a large extent for the tendency and extent of modification.

The question whether the peculiar problem of aquatic adaptation, especially as presented by the reptiles and mammals, is to aid us particularly in an understanding of evolutionary processes, and whether these paleontologic series are by reason of the peculiar limitations of environment especially significant, is yet to be definitely determined. We need first of all a much fuller understanding of all the living and extinct groups, and, following this, a much more exhaustive historical study of the whole problem than has thus far been undertaken.

AN ICHTHYOSAURIAN REPTILE FROM MARINE CRETACEOUS OF OREGON

The recent discovery by Professor E. L. Packard of two vertebral centra in the marine Cretaceous rocks of eastern Oregon marks the first occurrence of ichthyosaurian reptiles in the Cretaceous of the Pacific Coast region of North America. Although Cretaceous ichthyosaurs have long been known from England, France, East Indies, Australia, New Zealand and South America, their presence on this continent was not announced until 1905, when the senior author reported[1] them in the Benton formation of Wyoming. A second occurrence in the same region and in the same formation was recorded by the junior author[2] in 1914. Both of these records were based upon fragmentary specimens entirely adequate to establish their ichthyosaurian affinities, but insufficient to determine their generic affiliations.

The Oregon specimens likewise are too scanty for generic identification, but their geological occurrence intermediate between the well-known *Ophthalmosaurus* (*Baptanodon*) of the Sundance (Jurassic) and Upper Cretaceous ichthyosaurs of the Mowrey shales (Benton) makes their discovery of considerable scientific interest. With this extension of the known geographical and geological range of these Marine reptiles in North America, we may look forward to the discovery of better preserved material on which to base specific studies.

The materials of Professor Packard's find consist of one complete vertebral centrum and the lateral half of another. They were found about one-third of a mile apart in Mitchell Quadrangle, NE. ¼ Sec. 23, T. 11-S, R 21 E, Wheeler County, Oregon. Although the two centra are of approximately the same size, their occurrence so far apart would indicate probability of their pertaining to different individuals. The better preserved centrum is either the third or fourth of the cervical series, while the other is from the lumbar or posterior dorsal region. Viewed from the front, the cervical (figs. A

By John C. Merriam and Charles W. Gilmore. *Carnegie Institution of Washington Publication No. 393*, paper I, pp. 1–4, May 14, 1928.

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[1] J. C. Merriam, Science, n. s., vol. 22, No. 568, pp. 640–641.

[2] C. W. Gilmore, Science, n. s., vol. 39, No. 997, p. 210.

and B) is pentagonal in outline and much narrowed ventrally, with a slight suggestion of a hypophysial keel. The ventral contraction is pronounced, and in this respect the vertebra bears a striking resemblance to the atlas-axis complex of *Ophthalmosaurus.* The Oregon vertebræ are, however, fully one-third larger in all dimensions than the largest *Ophthalmosaurus* (*O. robustus* (Gilmore)) of which measurements are available.

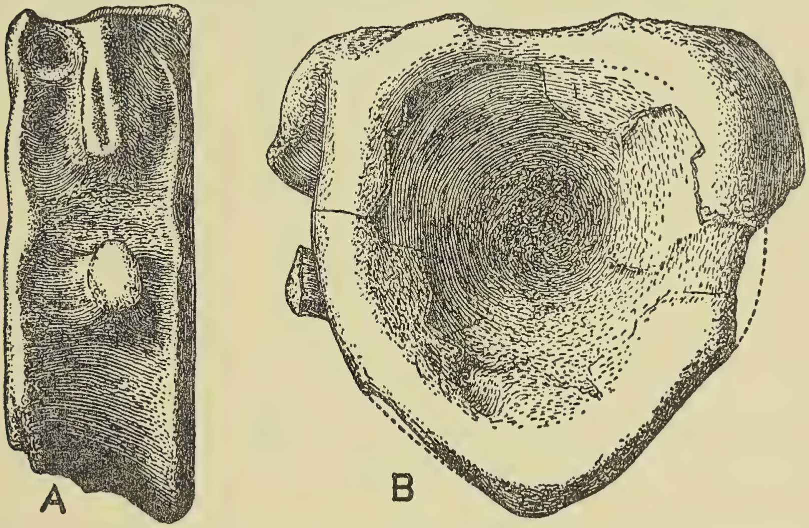

Fig. 1. Cervical vertebra of an ichthyosaurian reptile. A, viewed from right side; B, viewed from the front. One-half natural size.

Table of Comparative Measurements of Third Cervical Vertebræ

	Oregon specimen	*Ophthalmosaurus robustus* type	*O. icenicus*
	mm.	*mm.*	*mm.*
Greatest width of centrum, over all	137	100	....
Greatest width of centrum	111	....	66
Greatest height of centrum at center	127	....	74
Greatest antero-posterior diameter of centrum	45.7	34	28

In comparison with cervical vertebræ of other ichthyosaurians, no outstanding peculiarities in form or structure, beyond those mentioned, were observed, and this fact adds to the difficulty of determining their relationships.

These specimens may represent an ichthyosaur genus new to North America, but more clearly diagnostic materials are required before the affinities can be demonstrated.

MAMMALIA

FAUNA FROM THE JOHN DAY REGION OF OREGON

REPORT ON THE EXPEDITION TO THE JOHN DAY FOSSIL BEDS

The fossil field of the John Day region, in eastern Oregon, has been known to geologists for many years as one of most important of the numerous West-American localities furnishing good remains of Tertiary mammals. During the past thirty years the leading palaeontologists of the country have obtained from it large collections of remains, containing a great number of new and interesting animals. Professor Marsh of Yale, Professor Cope of Pennsylvania, Professor Condon of Oregon, Professor Scott of Princeton, and others, have personally conducted expeditions into the field. Beside these expeditions, professional collectors have worked over the ground during more than a dozen seasons. Excepting the collection of Professor Condon, at the State University of Oregon, the whole of the great amount of material accumulated has passed into the possession of a few of the large Eastern museums.

The John Day fossil beds are exposed in patches over a considerable area in Oregon, to the east of the Cascade range. The principal exposures being along the John Day River and its tributaries, the name of the river has been applied to them, and they are now known technically as the John Day system. Their age, as determined by comparison of the fossils with those of other systems, is generally supposed to be Miocene.

Our party, including Mr. F. C. Calkins, Mr. L. H. Miller, Mr. G. B. Hatch, and the writer, assembled at The Dalles, about May 20th, and, accompanied by Mr. L. S. Davis as guide, started in a southeasterly direction, aiming to enter the fossil fields near Bridge Creek. For about seventy-five miles our road lay almost entirely upon a vast lava field, which supports very little life, either animal or vegetable. In places this poverty is due to actual lack of soil, the surface of the ground being almost covered with weathered lava

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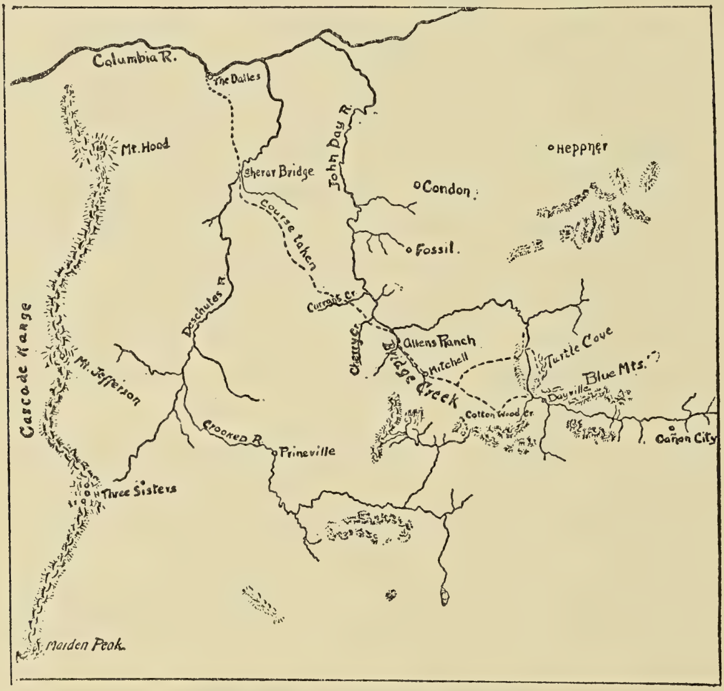
Science Association of the University of California, Proceedings of General Meetings, vol. 1, no. 1, pp. 3–10, 1899. Reprinted from the *University Chronicle*, vol. 2, no. 3, pp. 217–224, August 1899.

fragments. A large part of the region was, however, once good pasture land, supporting an abundance of nutritious bunch grass. The advent of the sheep has very greatly changed the whole face of the country. The pastures have been so thoroughly "sheeped" over that most unfenced areas are almost entirely denuded of the grass, which, being kept down too closely, has finally died out and does not return. With the grass have gone many of the smaller mammals, which were more or less dependent on it, and the snakes, which fed on the mammals. The old inhabitants think the rainfall has been considerably lessened by the destruction of the bunch grass. Certainly the manner in which the rain is disposed of when it does come is altered. Instead of being partially retained by the soil, as in years past, nearly the whole of the water from heavy showers goes off with a rush, changing the smaller streams into raging torrents, and not infrequently causing considerable damage to property or even loss of life.


Columbia R.
The Dalles
Mt. Hood
Sherar Bridge
John Day R.
Heppner
Condon
Fossil
Course taken
Currant Cr.
Deschutes R.
Cascade Range
Mt. Jefferson
Cherry Cr.
Allens Ranch
Mitchell
Bridge Creek
Turtle Cove
Blue Mts.
Dayville
Cotton Wood Cr.
Canyon City
Crooked R.
Prineville
Three Sisters
Maiden Peak

Outline Map of John Day Region

The region through which we passed, though underlaid by lava flows often of great lateral extent, is not an unbroken expanse of flat country, but has been broken up into several quite distinct areas by crustal movements which have taken place since the outpouring of the lava. As our party approached the Deschutes River from the west, we ascended a long, gentle slope. Within a mile or two of the river we came suddenly upon a reverse slope, which it is possible to descend on horseback at only a few points. This steep escarpment could be seen for a long distance to the north and south of us, the Deschutes keeping close to its foot to the north. From the bottom of this slope another extensive plain, seeming at a distance almost perfectly flat, stretched away to the north and east with a gentle upward slope to the southeast. At Currant Creek, forty-five miles to the southeast, after passing over this long slope, we came suddenly upon a second jumping-off place much like the first. Evidently the long, gentle, western slopes and steep escarpments toward the eastern side indicate, in rock of this character, the breaking up of an originally level region into blocks, which have tilted slightly to the west, giving the long, gentle slopes on that side, and the steep ones to the east, where they have been slightly elevated.

The Deschutes River, in fact all the rivers of this region, including the Columbia, have cut down sharply through the lava beds, forming magnificent gorges with almost vertical walls many hundred, in some cases several thousand, feet in height. Throughout the greater part of the lava country the streams are swift and full of rapids, and are rapidly deepening their cañons. Not having reached the stage at which they begin to widen their valleys, they do not materially affect the topography. The cañons on the plains are so narrow that they are almost hidden until one is fairly upon them.

From the top of the ridge at Currant Creek we obtained our first view of the fossil-bearing beds, also our best lesson in geology. The region immediately to the east is made up principally of older rocks, probably Mesozoic and Eocene, which are quite sharply tilted, and are cut by erosion into a multitude of irregular peaks and ridges. Twenty-five miles to the east we could just distinguish the nearly horizontal John Day beds, resting upon the older formations and covered in turn by a thick capping of lava. The older formations of this portion of the country have so far furnished no fossils, excepting some sub-tropical leaves, for which a new locality was discovered by our party.

The first working camp was located at Allen's ranch, on Bridge

Creek, in the partial shelter of a thick growth of sage brush. From that point numerous excursions were made into the surrounding country.

The exposure of the John Day beds at Bridge Creek is one of the best for studying the general geology of the deposits. The beds are here about fifteen hundred feet thick and are composed largely of volcanic materials mixed with sand and clay. They are nearly all strikingly colored, and probably vary somewhat in composition in the differently colored strata. At all the John Day exposures visited by our party the lowest beds were a deep red, the highest ones buff or white, and the intermediate strata blue or green. One of the results of our geological work was the determination of the persistence of these three sets of beds over the whole region. By means of these horizons we were enabled to study the vertical range or distribution in time of the animal species they contain.

From the character of the fossil remains found in the John Day beds, they are generally supposed to be deposits laid down in an inland sea or lake, once filling a somewhat irregular basin extending over a large part of eastern Oregon and portions of the adjoining states. The fossil remains consist of a few fresh water shells, a number of land shells washed into the lake by rains or streams, and the skeletons of a large number of vertebrates which were either drowned in the lake and buried entire in the mud, or, as was more frequently the case, which died upon the land, only portions of their dismembered skeletons being washed into the lake with the river or rain wash. Our study of the vertical distribution of the species in the beds brings out some interesting facts relating to the life about the lake during different periods of its existence. An example of this is found in the distribution of the rodents, which are found sparingly in the middle division and in the main portion of the upper beds, but are abundant at several localities, widely separated, in a stratum near the top of the upper beds. Evidently for some reason conditions were more than ordinarily favorable for the existence of small rodents about the lake at the time this stratum was being deposited, and they multiplied rapidly. The increase in the number of individuals was apparently accompanied by increase in the number of species.

How close to the time of the drying up of the lake the lava floods were poured over the deposits laid down upon its floor we do not know, but possibly a considerable interval separated these two events. The John Day beds show in some places evidence of erosion before being capped over. After the cooling of the lava there occurred the tilting of the crust blocks already mentioned.

One of the most interesting points in the geology of this region is found in the cutting of the streams. This gives us a measure of a portion at least of the time since the lava cap was completed. The rivers have evidently cut their present gorges through the lava, the fossil beds, and in some places into the older formations below since the lava floods cooled. Not the least interesting feature in the study of the fossils of this region in the field is the conclusive evidence, constantly before the collector's eyes, of the enormous length of time that has passed since the remains were entombed, as is shown by the thousands of feet of lake deposit and lava piled upon them, and by the great depth of the cañons cut since these great accumulations of strata were completed.

The Bridge Creek locality has probably been more thoroughly explored than any other in the country and has for that reason furnished a large number of fine specimens. The careful inspection of this and all the other good exposures by earlier expeditions made the work of our party very difficult, and we were dependent for our best finds upon specimens which had been only partially uncovered by weathering and had therefore more readily escaped notice. The best find of the party was made by Mr. Calkins on the evening of our first day here. A single tooth and a small fragment of bone protruding from the face of a steep cliff, when followed back into the rock, proved to be one side of the snout of a huge, extinct hog. The taking of this specimen into camp was the most difficult task of the expedition and occupied a portion of our party interruptedly for the first week and nearly all of us regularly for the second week. As we were pressed for time, we went forth day after day vowing to return at night with the skull. Thanks to the scientific instincts of the party, haste was made slowly and we were finally rewarded by seeing the skull reach camp practically uninjured. Many other good specimens, including a fairly complete skeleton of an *Oreodon*, one of the primitive even-toed ungulates, were discovered at Bridge Creek, but so much time was consumed in work on the large skull that other collecting suffered.

From Bridge Creek the party moved by slow stages to what is conceded to be the best and most extensive collecting ground in the region. This locality is situated in a widening of the gorge of the John Day beginning about three miles below the mouth of Cottonwood Creek, and has been called Turtle Cove by Professor Condon, who is its discoverer. On the road we visited a new locality for cretaceous fossils, discovered by our guide, Mr. Davis, and spent parts of two days collecting in what are known as the Loup Fork beds, on and near the John Day at Cottonwood. The Loup Fork beds, some hundreds of feet in thickness, rest upon the lavas over the John Day system and contain remains of a higher and more specialized fauna than that of the beds below the lava. The Loup Fork strata are mostly exposed in nearly vertical cliffs which weather very little, so that we were content to pick up a few good teeth and some limb bones, representing several species of horse, mastodon, rhinoceros, etc. The horse teeth serve to fill out a gap in the evolutionary series of horses already in our possession.

The entrance into Turtle Cove was effected with some difficulty, as the river just above it passes through a very narrow gorge, impassable except by boat. We found it necessary after fording the river to cross a high range of hills on a road which was for considerable stretches literally hidden by rocks averaging a foot or more in diameter. In the Cove two camps were made from which we worked a number of the best exposures. The largest outcrop, called by us the Blue Basin, is a veritable labyrinth of cañons, gulches, and caves cut into the soft blue rock of the middle John Day beds by the heavy rains. The coloring of these beds is frequently most wonderful and of the most delicate shades. Passing along the bottom of any of the larger cañons, the wilderness of finely sculptured and delicately-tinted peaks and pinnacles about frequently causes one involuntarily to pause and gaze, astonished that even nature could produce such magnificent architecture.

As the result of our collecting in Turtle Cove, we have several dozen skulls of larger mammals and about as many more of small rodents, besides many good specimens of teeth, limbs, vertebrae, etc. The best specimens include a nearly complete skull of a three-toed horse (*Anchitherium*), fine specimens of two extinct wolves, a rhinoceros, many *Oreodons*, a primitive deer, several turtles, etc.

Our geological studies, begun at Bridge Creek, were here continued, and without exception the previous observations on the sequence of the beds of the system were confirmed. Mr. Calkins made a complete collection of the rocks of the region for the petrographical museum and Mr. Miller, whose time was partly devoted to zoölogical work, collected a large number of birds, mammals, and reptiles.

On the return trip we crossed the mountains to the west of the Cove, and, regaining the stage road near Mitchell, passed over the same territory covered on the way out.

Though some of the scientific results of the expedition have already been briefly mentioned, it should perhaps be stated that our collections have not yet been really studied, as the business in the field is mainly to acquire. The careful preparation of the specimens, requiring many months of work, must be completed before exact study of the relationships and history of the species can begin.

CLASSIFICATION OF THE JOHN DAY BEDS

Classification of the John Day beds. By JOHN C. MERRIAM, Berkeley.

The John Day beds average about fifteen hundred feet in thickness, and apparently contain a very large proportion of volcanic materials. They seem to rest unconformably on a thick series of plant bearing, fresh water beds, which have been considered Eocene. The Columbian lavas rest apparently unconformably upon the John Day beds.

On the basis of lithologic and stratigraphic characters, the John Day System may be divided into three divisions, lower, middle, and upper John Day. The lower beds are mainly colored a brilliant red, seem to have suffered more disturbance than the higher beds and are practically barren of fossils. The middle beds are blue, green or drab, and are in places quite fossiliferous. The upper beds are buff or white. They are largely made up of volcanic material. Many fossils have been obtained from this division. One horizon particularly is rich in rodent remains.

The writer's study of the vertical range of the John Day species has not progressed far enough to permit of any definite statement regarding their zonal arrangement. Professor J. L. Wortman has already proposed the division of the system, on faunal grounds, into upper *Merycochoerus* and lower *Diceratherium* beds. The use of the lithologic divisions here proposed will greatly aid in the study of the vertical range or history of John Day species.

Abstract of paper presented at first annual meeting of the Cordilleran Section, Geological Society of America, San Francisco, December 29 and 30, 1899. *Science*, n. s., vol. 11, no. 267, pp. 219-220, February 9, 1900.

GEOLOGICAL SECTION THROUGH JOHN DAY BASIN[1]

The John Day river and its tributaries have exposed in the erosion of their canyons about 10,000 feet of strata, giving a full series of formations from Lower Cretaceous to Quaternary.

The oldest rocks in this region which are known to the writer are a series of altered sedimentaries in the northeastern part of the basin. They are pretty certainly of pre-Cretaceous age and are underlain by quartz diorite,[2] which is presumably intruded into them.

On Bridge creek, near Mitchell, a great thickness of Cretaceous is exposed. The lower 2,000 to 3,000 feet of this section are typical Knoxville. The upper 1,000 to 2,000 feet are Chico.

Resting upon the Chico, near Mitchell, also showing typical exposures at Clarnos ferry, is a presumably Eocene formation, to which the name Clarno is given. This formation is made up entirely of tuffs, ashes, and lavas. In places it contains many plant remains and is apparently in part a fresh-water formation.

The John Day formation rests directly upon the Clarno at Clarnos ferry. The basin in which it was deposited is quite different from that of the Clarno. It probably rests unconformably upon that formation. The Lower John Day beds are considerably contorted in some localities. Ordinarily they are colored a deep red. Fossils remains are exceedingly rare in this division.

The blue-green beds of the Middle John Day are very fossiliferous. They correspond to the Diceratherium beds of Wortman. The Upper or Buff beds of the John Day lap over the middle division and rest in places upon the older formations. The upper division corresponds to the Merycochœrus beds of Wortman. As *Merycochœrus* does not occur in the John Day, the upper division will be called

Abstract. *Bulletin of the Geological Society of America*, vol. 12, pp. 496–497, November 21, 1901.

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[1] The paper was illustrated with lantern slides showing the principal formations and their relations to each other.

[2] Determined by Frank C. Calkins.

the Paracotylops beds. This name is based on the new generic name proposed by W. D. Matthew for the Upper John Day oreodons, originally supposed to be *Merycochœrus*.

The Columbia lava, an extension of the lavas on the Columbia river to the north, rests unconformably on the crumpled John Day formation. The name Columbia lava should be restricted to this horizon of the lavas in this region, as other beds included in this group belong in some cases to different geological periods.

The Cottonwood (Loup Fork) formation, near 1,000 feet in thickness, rests on the Columbia lava. The Van Horn Ranch plants, which have generally been considered as John Day, are from this horizon. Remains of a true John Day flora, which had not previously been known, were discovered by the University of California expedition in 1900. The discovery of the true stratigraphic position of the Van Horn Ranch flora explains the apparent inverted position of the Neocene formations in central Washington.

Resting on the worn edges of the Cottonwood beds is the Rattlesnake formation, comprising several hundred feet of gravel, tuff, and lava.

In canyons cut through the Rattlesnake and Cottonwood are several terraces. Remains of elephants and later horses found in the lower terrace deposits show that they were formed in Quaternary time.

A CONTRIBUTION TO THE GEOLOGY OF THE JOHN DAY BASIN

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University of California, Bulletin of the Department of Geology, vol. 2, no. 9, pp. 269–314, pls. 6–8, April 1901.

Introduction

During the summer seasons of 1899 and 1900, the writer traveled over a considerable part of the John Day basin, while in charge of palæontological expeditions sent out from the University of California to collect vertebrate fossils. The following discussion of the geology contains the results of observations made while engaged in that work.

Though the object of the expeditions was the acquisition of specimens, much of the value of the material being dependent on the circumstances of its occurrence, efforts were made from the beginning to determine, as accurately as possible, the stratigraphic relations of the fossil-bearing beds.

In looking over the literature bearing upon John Day geology, before visiting the field, the writer was considerably surprised to find that only a few short paragraphs relating to the subject had ever been published, and that in many of the most important particulars these accounts were decidedly contradictory.

In view of the disagreement among observers regarding the geological history of the region, it was perhaps to be expected that no single account would be found to agree with the facts. The first season's work in the field demonstrated that this was actually the case, and showed the necessity of working out the true stratigraphic succession as an indispensable preliminary to satisfactory palæontological work. With this object in view, as much information was gathered as could be obtained without interfering seriously with the main work of the expeditions.

Future investigations will certainly show that very many important things have been overlooked, and doubtless many weaknesses in the present discussion will be pointed out; the writer's purpose will, however, be accomplished if the general stratigraphic succession and the sequence of major geological events are here set forth in such a manner as to make intelligible discussions of the extinct faunas and floras of this region which will follow this paper.

The writer is indebted to Mr. F. C. Calkins for all petrographical determinations mentioned in this paper. Mr. Calkins has now in preparation an article on the rocks of the John Day region.

Mr. V. C. Osmont has contributed some valuable information concerning the geology of the region south of the Blue Mountains.

To Dr. T. W. Stanton the writer is under obligation for the contribution of a note on the Cretaceous fossils collected at Spanish Gulch.

Prof. T. H. Knowlton has kindly undertaken the study of the fossil plants obtained by the University expeditions, and furnishes for the paper tentative lists of species with a brief discussion of the affinities of the floras. In a bulletin of the U. S. Geological Survey, which is now in preparation, Professor Knowlton will present a discussion of the John Day floras based on a study of all of the collections which have been obtained from that region.

Geographic Features

The existing John Day basin of north central Oregon is a well-defined area almost completely surrounded by the triangular Blue Mountain Range. The rugged eastern ridges, rising to an elevation of over 6,000 feet, are composed largely of pre-Tertiary formations which have been much disturbed. To the west the ranges are made up principally of Tertiary lavas forming regular and frequently flat-topped ridges somewhat lower than those to the east.

Inside the basin are a number of smaller ridges and plateaus, among which the John Day and its tributaries wind in deep and often narrow cañons. The streams have here laid bare magnificent sections of all the basin formations, affording unexcelled opportunities for stratigraphic and palæontologic studies.

The main John Day River leaves the west side of the basin through a gap between the north and south ranges of the Blue Mountains. From this point it flows approximately north to the Columbia. Tracing the river back from the gap, its course is seen to be nearly east, till, at the lower end of Turtle Cove, it is divided into two streams, known as the North Fork and the main river. As the North Fork is the larger stream, the writer has fallen into the habit of calling the southern branch the South Fork. At Dayville the South Fork divides into two streams, of which the southern is known as the South Fork and the other as the main river. To avoid confusion the writer will refer to the northern branch here as the East Fork. The course of the South Fork from Dayville is across the southern range, to the south of which it occupies a small basin which the writer has not visited.

Excepting the mountain ranges and some of the highest interior ridges, which support a heavy growth of pine timber, the country is only sparingly wooded. A fringe of cottonwoods, birches, and willows along the streams, and a few scattered junipers comprise the most important part of its sylva. The basin is mainly an open grass country with a sprinkling of sagebrush on the bottom-lands. Some years ago a rich growth of bunch-grass over a large part of the area supported large herds of cattle. Latterly the sheep industry has overshadowed all others and the grass has been rapidly disappearing.

History of Exploration[1]

The existence of fossil mammalian remains in Eastern Oregon seems to have been first noticed by a company of soldiers which passed through that region in 1861. When the party reached The Dalles on its return journey, a number of the men had with them fragments of bones and teeth obtained from fossil beds in the Crooked River country. The only specimen brought back by this party, of which any definite information is now obtainable, was a fine rhinoceros jaw, which was in the possession of Lieutenant Waymire.

Prof. Thomas Condon, who was then pastor of the Congregational Church in The Dalles, saw the fossils and obtained from the members of the party considerable information concerning their occurrence. Condon immediately concluded that an important field for palæontological research had been discovered and made use of the first possible opportunity of visiting the beds. Early in the next year he was allowed to go with a company of soldiers taking supplies across to Harney Valley. On the road out, he passed through the Crooked River country and obtained a few fossils there. On the return trip, made by the way of Camp Watson, he discovered the large exposures at Bridge Creek and supposed them to be of the same system as the Crooked River beds.

In passing through the John Day country on his return journey, Condon met Sam Snook, a resident of the region who had already taken some notice of the fossil bones, and engaged his service as a collector.

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[1] The writer is indebted to Prof. Thomas Condon for the greater part of his information concerning the discovery of the fields. Mr. L. S. Davis, who has accompanied nearly all of the expeditions, contributed most of the facts concerning the later exploration.

The following summer, 1863, found Condon again collecting and exploring at Bridge Creek and along the John Day.

In 1864, probably in company with Snook, he first saw the large exposures of John Day strata in what he has named Turtle Cove.

In 1870, or '71, some specimens of teeth from the John Day beds were sent by Condon to Prof. O. C. Marsh. Almost immediately he received a request from Marsh to guide an expedition from Yale into the new field. Marsh came out with a party of fifteen or sixteen persons in the fall of 1871, and under Condon's guidance visited some of the most important localities. A small amount of collecting was done in what are now known as the John Day and Mascall beds, but the work was chiefly reconnaissance. While in the field Marsh engaged several collectors to carry on the work for him. Systematic collecting began in the following spring and was continued practically without interruption till 1877. Most of the work during this period was done by L. S. Davis and William Day, who explored practically all of the exposures in the region.

Early in the winter of 1871, shortly after Marsh's visit to the field, Lord Walsingham, William de Gray, while on a hunting expedition, passed through the fossil fields and obtained some valuable specimens at Turtle Cove and on Bridge Creek. His small collection was presented to the British Museum and furnished material for Bettany's[2] valuable contribution to our knowledge of the John Day Oreodontidæ.

In the summer of 1873, Prof. Joseph Le Conte,[3] in company with Professor Condon, visited the western border of the field and made some important observations on the geology.

Parties under Wortman and Sternberg collected for Prof. E. D. Cope in 1878 and 1879, obtaining the material upon which Cope based his important publications on John Day vertebrates.

In the summer of 1880, Captain Bendire, of the U. S. Army, with a large party of the 7th U. S. Cavalry, made a short tour through the basin under the guidance of L. S. Davis. Collections of plants were made by him at Bridge Creek, Van Horn's Ranch, and probably also at Cherry Creek. A few fish remains were collected in the plant beds at Van Horn's Ranch and small collections

[2] G. T. Bettany. On the Genus *Merycochœrus*, Quar. Jour. Geol. Soc. Lond., 1876, V. 32, p. 259.

[3] Am. J. Sc., 1874, Vol. 7, p. 167.

of mammalian material were obtained at several localities in the John Day and the Mascall formations. Through some unfortunate mistake, Bendire's collection of plants and fish from the Mascall seems to have been considered as coming from below the John Day, and dire confusion has been the result of all geological publication based upon that supposition. Bendire's collections were turned over to the Smithsonian Institution. The plants were afterwards described by Lesquereux,[4] and the fish by Cope.[5]

In 1882, Davis and Day collected under Marsh for the U. S. Geological Survey. Their work seems to have been confined to the beds south of the Blue Mountains.

No farther work was done in the field till 1889, when Prof. W. B. Scott spent the summer in the John Day basin with a large party from Princeton University. After Professor Scott's return a portion of his party worked over the country south of the mountains.

LITERATURE

The first mention of the fossiliferous deposits in the John Day basin which appears in the literature was made by Dr. Joseph Leidy. In October, 1870, Leidy presented before the Philadelphia Academy of Sciences[6] a short paper, in which he described "a collection of fossils recently received for examination through the Smithsonian Institution, from Rev. Thomas Condon, of Dalles City, Oregon." The collection consisted of "remains of mammalia obtained by Mr. Condon from the valley of Bridge Creek" (and "Big Bottom of John Day"), "a tributary of John Day's River, Oregon." The collection included new forms of *Paracotylops* (*Merycochœrus*), *Rhinoceros*, and *Anchitherium*. New occurrences of *Agriochœrus*, *Leptomeryx*, *Lophiodon* (?), *Elotherum*, and a Dicotyles-like form were also noted. Most of the previously-known species, as identified by Leidy, were forms belonging to the White River fauna, and he probably considered the John Day beds as of nearly the same age as the White River.

In 1873 Professor Marsh described[7] several new fossil mammals obtained by his exploring party in the John Day country in 1871.

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[4] Proc. U. S. Nat. Ins., 1888, pp. 13–19.

[5] Am. Nat., 1889, p. 625.

[6] Proc. Phil. Acad., 1870, p. 112.

[7] Am. Jour. Sc., 3d ser., Vol. 5, p. 409.

He referred two forms to the Miocene and one to the Pliocene, thus making the first statement regarding the age of the beds.

In his paper on the great lava flood of the West, Prof. Joseph Le Conte[8] makes the first mention of the structural relations of the John Day formations. His statement regarding the relation of the lava to the John Day beds is in part as follows: "The lava in this region is . . . underlaid by the remarkable fossiliferous Miocene lake deposit of the John Day Valley; erosion has cut through the lava cap into the soft strata beneath."

The earliest general discussion of John Day geology which appears in the literature is the following statement published by Marsh[9] in 1875.

"The Blue Mountains formed the eastern and southern shores of this lake, but its other limits are difficult to ascertain, as this whole country has since been deeply buried by successive overflows of volcanic rock. It is only where the latter have been washed away that the lake deposits can be examined. The discovery and first explorations in this basin were made by Rev. Thomas Condon, the present state geologist of Oregon. The typical localities of this Miocene basin are along the John Day River, and this name may very properly be used to designate the lake basin. The strata in this basin are more or less inclined and of great thickness. One section near the John Day River, examined by the writer in 1871 and again in 1873, seems to indicate a thickness of not less than 5,000 feet. The upper beds alone of this series correspond to the deposits in the White River basin. The lower portion also is clearly Miocene, as shown by its vertebrate fauna, which differs in many respects from that above. Beneath these strata are seen, at a few localities, the Eocene beds containing fossil plants mentioned above. They are more highly inclined than the Miocene beds, and some of them show that they have been subjected to heat. The inferior strata elsewhere are Mesozoic, and apparently Cretaceous. Above the Miocene strata Pliocene beds are seen in a few places, but basalt covers nearly all."

In this account we find the name "John Day" first used for the principal fossil beds of the basin. The relation of this horizon to the great lava beds is also correctly stated, though it is not quite clear

[8] Am. J. Sc., 1874, Vol. 7, 3d ser., p. 167.

[9] Am. J. Sc., 1875, 3d ser., Vol. 9, p. 52.

whether he considered the Pliocene as also covered by the basalt flows. The Pliocene referred to is pretty certainly the Mascall beds. It is known that Marsh camped near the typical exposure of this formation and did some collecting in it. To what Marsh referred in his statement concerning Eocene and Cretaceous it is not certain. He has, however, correctly described the stratigraphic sequence.

In 1880 Prof. E. D. Cope[10] published the following statement concerning the geology of the John Day country:—

"The regions of the John Day River and Blue Mountains furnish sections of the formations of central Oregon. Above the Loup Fork or Upper Miocene there is a lava outflow, which has furnished the materials of a later lacustrine formation, which contains many vegetable remains. The material is coarse, and sometimes gravelly, and it is found on the Columbia River, and I think also in the interior basin. Professor Condon, in his unpublished notes, calls this the Dalles Group. It is in turn overlaid by the beds of the second great volcanic outflow. Below the Loup Fork follows the Truckee Group, so rich in extinct mammalia, and below this a formation of shales. These are composed of fine material, and vary in color from a white to a pale brown and reddish-brown. They contain vegetable remains in excellent preservation, and undeterminable fishes. The *Taxodium* nearly resembles that from the shales at Osino, Nevada, and on various grounds I suspect that these beds form a part of the 'Amyzon Group' (American Naturalist, June, 1880), with the shales of Osino and of the South Park of Colorado. Below these, is a system of fine-grained, sometimes shaly, rocks of delicate gray, buff, and greenish colors, containing calamites, which Professor Condon calls the *Calamite* beds. Their age is undetermined."

In spite of Cope's assumption that the plant and fish-bearing beds mentioned by him were to be correlated with his Amyzon[11] group, Lesquereux[12] referred the collections from Van Horn's Ranch to the late Miocene. In a later statement regarding the John Day stratigraphy,[13] Cope speaks of the calamite beds as doubtless belonging to the Triassic or Jurassic. This horizon was determined by Lesquereux as Eocene.

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[10] Cope, Proc. Am. Phil. Soc., 1880, p. 61.

[11] E. D. Cope, Am. Nat., 1879, p. 332. Late Eocene or Early Miocene, Nevada.

[12] Proc. U. S. Nat. Mus., 1888, p. 13.

[13] Hayden, Surv. Terrs., Vol. 3, p. 16.

In a recent bulletin by W. D. Matthew[14] on a provisional classification of the fresh-water Tertiary of the West, there appears the statement that the Mascall formation (Cottonwood beds) is separated from the lower beds (John Day) by a basaltic flow. The loose gravels above the Mascall are also separated as a definite horizon.

In 1898 Wortman proposed the division of the John Day beds into the upper or Merycochœrus beds and the lower or Diceratherium beds.

General Features of the Geology

The section of the John Day formation, as it is known to the writer, includes at least nine formations, showing the following sequence:—

River terraces, with undisturbed Quaternary fossils.
Rattlesnake formation. Gravels, ash, tuff, and rhyolitic lava.
Mascall formation. Ashes, tuffs, and possibly gravels.
Columbia lava. Basaltic flows.
John Day series. Ashes, tuffs, and rhyolite flows. Sands and gravels near the top. Lower, middle and upper divisions.
Clarno formation. Ashes, tuffs, andesitic and rhyolitic lavas.
Chico formation. Sandstones and conglomerates.
Knoxville formation. Black shales.
Pre-Cretaceous sedimentaries, serpentines. Granitic masses of unknown age.

The Knoxville and Chico are marine formations. It is not improbable that some of the eruptives below the Cretaceous have been intruded into it, though some of them are pretty certainly older than the Knoxville. From the Clarno formation to the top of the series, excepting a very small portion of the whole thickness, the deposits are made up of eruptive materials. The Clarno, John Day, and Mascall are almost entirely composed of ashes and tuffs. They have generally been considered as being wholly lake deposit, but, as will be shown later, the character and occurrence of the fossil remains which they contain are such as to make it doubtful whether they owe their origin solely to this mode of accumulation.

The Rattlesnake deposits also contain a large proportion of erupted material, but it is mainly composed of gravels derived from the Columbia lava.

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[14] Bull. Am. Mus. Nat. Hist., Vol. 12, p. 19, 1899.

At the close of a long era of erosion following the Rattlesnake epoch, a series of terraces was formed along the main streams. Undisturbed Quaternary remains give definite evidence regarding the age of these deposits.

The surface formation over the greater part of the basin is the Columbia lava, which has covered the whole region from the Cascades to the eastern Blue Mountain ranges. At points where the writer has been able to examine them, the existing northern and southern ranges are capped with a considerable thickness of Columbia lava. Ridges may, however, have existed in this region as early at least as the beginning of the Miocene, since the John Day deposits are either absent or much thinner along the existing ranges.

The Mascall beds are exposed principally in the southern part of the basin and south of the Blue Mountains. They are usually covered by a considerable thickness of Rattlesnake beds in which a rhyolite flow has been the main protection against erosion. The Rattlesnake beds are also confined, so far as the writer is acquainted with them, to the southern region. Exposures of the John Day beds and other pre-Columbia lava formations are found only along the streams, where the lava has been cut through.

Pre-Cretaceous Formations

The oldest fossil-bearing strata which have been found in the John Day basin north of the southern Blue Mountain range are of Cretaceous age. At several points in the basin formations have, however, been found which have the appearance of being much older than the Cretaceous beds.

In the northeastern part of the basin a considerable area of quartz diorite is exposed on the Middle Fork, about five miles above Ritter. Where it was crossed by the writer, it is bordered by sedimentary rocks which show a degree of induration and deformation not met with in the Cretaceous where it has been seen in the basin. On Desolation Creek to the northeast of the diorite area, this series seems to be extensively developed, and would, doubtless, repay careful study.

Opposite the Powell place, four or five miles above Ritter, on Middle Fork, fossiliferous middle Tertiary beds rest upon the older series. Columbia lava here covers the fossil beds and also laps over upon the diorite, from which it is separated by only a thin bed of ash.

At Spanish Gulch, twelve miles southwest of Dayville, the Chico Cretaceous is seen resting upon serpentine, which has the appearance of being intruded into it. At the head of the gulch the serpentine is separated from what was taken to be Chico conglomerate by a zone of schist and quartzite. Not far from this locality there is associated with the serpentine a considerable thickness of quartzite with quartz veins, which have produced some gold. Limestones quite different from any seen in the Chico are also exposed here. From the same neighborhood the writer obtained a specimen of a granitic rock, said to form one wall of a tunnel.

Though no direct proof can be presented, it seems probable that some of the rocks associated with the serpentine at Spanish Gulch are older than the Cretaceous.

At the junction of Muddy and Currant Creeks, six miles south of Clarno's Ferry, there are exposed several hundred feet of black slates showing a dip of about 20° to the northeast. At the mouth of Muddy Creek the cleavage of the slates runs almost east and west across the obscure bedding of the formation. On several occasions as parties have been passing through the region, search has been made in these beds for fossils, but so far no traces of them have been found. Judging from the appearance of this formation, it is older than the Knoxville shales.

Near the head of the Crooked River, south of the Blue Mountains, there are said to be exposures of Palæozoic, Triassic, Jurassic, and Cretaceous formations.

Cretaceous, Chico and Knoxville

Exposures of Cretaceous formations are to be found at several points on the western side of the basin. The best outcrops are seen at Mitchell and Spanish Gulch. At Spanish Gulch a considerable thickness of conglomerate and sandstone, dipping about 30° to the southwest, is found above the serpentine. Fossils are quite numerous in this formation, and considerable collections were made at two localities. All the material obtained was placed in the hands of Dr. T. W. Stanton, who has kindly furnished the following report:—

"The fossils come from two localities at Spanish Gulch, and only about three-fourths of a mile apart. The larger part of the collection is from locality 814, well up on mountain at Spanish Gulch, Dp. 27°S. of W. This lot contains the following species:—

Anomia sp.
Mytilus sp. cf. *M. lanceolatus* Sowerby.
Trigonia leana Gabb.
Trigonia evansana Meek.
Meekia radiata Gabb?
Nucula (*Acila*) *truncata* Gabb.
Meretrix varians Gabb.
Meretrix sp. a.
Tellina ashburneri Gabb.
Tellina skidegatensis Whiteaves.
Asaphis multicostata Gabb.
Homomya concentrica Gabb?
Mactra? sp. a.
Corbula traskii Gabb.
Dentalium stramineum Gabb.
Gyrodes expansa Gabb.
Cinulia? sp.
Desmoceras dawsoni Whiteaves?

"Locality 813, west of locality 814 about three-fourths of a mile and probably higher in the section, yielded the following forms:—

Anomia sp.
Trigonia evansana Meek.
Chamidæ gen. et sp. ind.
Meretrix varians Gabb.
Meretrix? sp. b.
Tellina ashburneri Gabb.
Mactra? sp. b.
Corbula traskii Gabb.
Dentalium sp.
Scalaria clementina (Michelin)?
Solarium? sp.

"From the number of species in common it is evident that the fossils from the two localities belong to the same general fauna, though there might be some difference in horizon as their field relations seem to indicate. *Trigonia evansana*, *Meretrix varians*, and *Corbula traskii* apparently range throughout the Chico beds.

"A few of the names in the above list deserve a word of special comment.

"*Mytilus* cf. *lanceolatus* Sowerby. Represented by a single small specimen that seems to be identical with form from Skidegate Inlet, Queen Charlotte Islands, doubtfully referred by Whiteaves to *M.*

lanceolatus. It also occurs at Texas Springs, California, and Jacksonville, Oregon.

"*Trigonia leana* Gabb. This is the species figured by Gabb in Paleontology of California as *T. gibboniana* Lea. He afterward considered it a new species and named it *T. leana*, but there is still reason to doubt whether it is really distinct from *T. tryoniana* Gabb which was described from an imperfect specimen that had lost the outer layer of shell. Some of the shells in the present collection have lost the outer layer of shell and thus acquired such a different aspect that they were at first considered a different species. *T. leana* occurs in the lower Chico beds at Jacksonville, Crooked River, Grave Creek, and other localities in Oregon, and at many places in California, including Texas Springs and Horsetown. The fossils from Skidegate Inlet, listed by Whiteaves as '*T. tryoniana?*' probably belong to *T. leana*, if it is really distinct from the typical *T. tryoniana*. If not, the latter name has priority, and should be used for the species.

"*Meekia radiata* Gabb? This species is represented by a number of well-preserved specimens differing materially from the figures of Gabb's type in that they attain a much larger size, being as large as *M. sella* Gabb, and have the whole surface covered with radiating sculpture. Specimens of smaller size but with precisely similar sculpture have been collected at Texas Springs, California, and the same form occurs at Grave Creek, Oregon, associated with others in which the surface is partly exfoliated and the radiating sculpture is very obscure. These facts lead to the suspicion that *M. radiata* was based on the miniature or depauperate specimens, in which the surface was not perfectly preserved, and I have, therefore, not ventured to separate these larger well-preserved specimens as a distinct species.

"*Chamidæ*. There are several small fragments apparently belonging to an undetermined genus of Chamidæ, showing a structure similar to *Coralliochama*, but not identical with it.

"*Meretrix varians* Gabb. This variable species is widely distributed in the Chico. Whiteaves cites from Vancouver Island, under the name *Cytherea nitida* Gabb.

"*Tellina skidegatensis* Whiteaves. The collection contains a number of specimens referable to this species which was described from Bearskin Bay, Skidegate Inlet, Queen Charlotte Islands.

"*Asaphis multicostata* Gabb. This species, originally described from Crooked River, Oregon, is represented by a single imprint. *Linearia suciensis* Whiteaves is similar in form and sculpture and may be based on the same species.

"*Homomya concentrica* Gabb. The specimen in the collection is much larger than Gabb's figure and differs somewhat in form, but it is probably like the large specimens which he doubtfully referred to the species, and like those cited from the Sucia Island by Whiteaves. It is certainly identical with a form in the Geological Survey collection from Texas Springs, California.

"*Scalaria clementina* (Michelin)? The single fragmentary specimen appears to be identical in form and sculpture with the Queen Charlotte Islands species that Whiteaves[15] has listed under this name, and earlier figured as *S. albensis* (?). The same form occurs at Texas Springs.

"*Desmoceras* (*Puzozia*) *dawsoni* Whiteaves. A single fragment of an Ammonite in the collection agrees very well with the figures of this species from Queen Charlotte Islands formerly referred to *Haploceras beudanti* but recently named as above.[16]

"The whole assemblage of forms in the above lists indicates a horizon at or very near the base of the Chico formation. A similar fauna, with some additions, occurs in the sandstones at Texas Springs and near Horsetown, Shasta Co., Cal., and has been regarded as proof of the blending of the Shasta and Chico faunas,[17] partly because the beds at Horsetown had long been thought to belong to Gabb's Shasta group, and had even given the name, Horsetown beds, to the upper division of the Shasta. It is evident, however, from White's somewhat vague definition of the Horsetown beds that the term was meant to include the strata immediately above the Knoxville that contain the fauna so well developed on the north fork of Cottonwood Creek, in the neighborhood of Ono, and which really has no close relationship with this basal Chico fauna of Texas Springs, Horsetown, and elsewhere. The confusion has, doubtless, been increased by incorrect identifications of fragmentary fossils. It is not intended to deny that there are species common to the Horsetown and Chico faunas, but when the formations are properly restricted the number of common species is not as great as I once supposed, and the sandstones at Horsetown and Texas Springs containing the above-mentioned fauna belong to the Chico rather than to the Horsetown.

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[15] Mesozoic Fossils, Vol. I, pt. IV, p. 287, Ottawa, 1900.

[16] Mesozoic Fossils, Vol. I, pt. IV, p. 286.

[17] Stanton, The Faunas of the Shasta and Chico Formations, Bull. Geol. Soc. Am., Vol. IV, pp. 245–256.

"This lower Chico horizon is known to occur at a number of localities in Oregon, as Jacksonville, Grave Creek, and Crooked River, usually resting unconformably on pre-Cretaceous rocks. The beds at the ''49 Mines' near Phœnix, Oregon, described by Anderson, probably represent about the same horizon. From the fossils published by Whiteaves it seems that this horizon probably occurs in the Queen Charlotte Islands on the shores and islands of Skidegate Inlet and probably of Cumshewa Inlet, where it has been grouped in the 'lower shales and sandstones' with beds that are considerably older. During the last field season I have seen evidence that it is also represented, though with a different faunal facies, in Los Angeles and Riverside Counties, Southern California. In this region, as at many of the northern localities, it is not accompanied by older Cretaceous beds, thus indicating a general and widespread transgression of the sea upon the land at the beginning of the Chico epoch."

At Mitchell, about eighteen miles northwest of Spanish Gulch, there is exposed a thick section of sandstone, conglomerate, and shale, lying below an early Tertiary formation. The upper portion of this section is made up of sandstones and conglomerates resembling the Chico at Spanish Gulch. The lower beds are shale, with only an occasional harder stratum. The lithological characters of the lower divisions exactly duplicate those of the Knoxville as it is usually developed in California and south central Oregon. The shale seems to be capped by gravels and contains in the midst of the section a great mass of an unknown eruptive.

The total thickness of the two formations could hardly be less than three or four thousand feet, of which the shales appear to make up the larger part. The whole section is finely exposed in the bluffs along Bridge Creek at Mitchell. It dips 20° to 30° to the southeast and probably forms the west side of a syncline of which the Spanish Gulch exposure is the other limb. The whole area between Spanish Gulch and Mitchell is covered by Tertiary.

At the lower end of the Knoxville section the dip of the shales changes to westerly. Only a small portion of the western limb of this anticline is however exposed, as the Tertiary formations mantle over it.

Eocene, Clarno Formation

At numerous localities along the western side of the John Day basin, there are exposed, either below the lowest John Day beds or above the Chico Cretaceous, several hundred feet of strata which certainly do not belong to either of these horizons. To these beds the name Clarno formation has been applied by the writer.[18]

Typical exposures of the Clarno are to be seen at Clarno's Ferry on the John Day east of Antelope, near the town of Fossil, on Cherry Creek, and near Burnt Ranch.

The Clarno formation is made up almost entirely of erupted materials. Part of the section consists of rhyolite and andesite flows, but the most characteristic portion comprises sedimentary beds grading from ashy shale to coarse tuff. The ash and tuff beds frequently contain plant remains in abundance and were evidently, at least in part, deposited in water. The strata seem in some places to have accumulated very rapidly. At one locality where large specimens of *Equisetum* have been found in shaly beds, the stems are standing erect and cutting across the stratification planes. This could occur only where deposition or shifting of the ashy mud was taking place very rapidly. The wide extent of the plant beds, which seem to be present at nearly all of the well-known occurrences of the formation, indicates the existence of lacustrine conditions, intermittently at least, over this region during the Clarno epoch.

The thickness of the Clarno formation is not less than 400 feet. It will probably be found to exceed that limit. The strata are usually gray to buff but sometimes show brilliant coloration in shades of red, green, and blue.

The relations of the Clarno to the Cretaceous may be seen just east of the town of Mitchell, where a considerable thickness of andesite and tuff is resting upon the Chico. Again, on the wagon road between Allen's Ranch and Mitchell, the Clarno appears to rest upon the western side of the Knoxville anticline.

Where the Clarno has been found in contact with the John Day there is no apparent angular unconformity of the strata. The difference in induration and weathering is, however, very noticeable. The sedimentary parts of the Clarno show a much greater degree of induration than the John Day beds immediately above, and tend at all localities to form steep bluffs ornamented frequently with balanced rocks or grotesque figures. The soft beds of the Lower John Day normally weather into rounded, mud-covered domes or more gently sloping banks.

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[18] Jour. Geology, Jan.-Feb., 1901, Vol. IX, p. 71.

On the river above Clarno's Ferry, this formation dips about 15° to 25° to the north and beneath the Lower John Day. Fine exposures continue along Pine Creek east of the Ferry. North of the town of Fossil the Clarno is again seen typically developed and dipping under the John Day. Along Currant Creek it is well exposed and is close to, or in contact with, the Columbia lava.

At most of the localities mentioned the Clarno shows a considerable thickness of lava beds toward the top. These flows are not, however, the uppermost part of the section. The base of the formation is formed by andesite flows in several places but it was not determined whether the whole section is present at these points.

At most of the Clarno localities where careful collecting has been done, plant remains are found to be fairly abundant. Repeated attempts have been made to obtain vertebrate or invertebrate fossils also, but, so far as the writer is aware, none have ever been discovered. The plants are, perhaps, most common in a bed of tuff and ash, 100 or more feet in thickness, belonging to the middle or the lower part of the formation. The remains from Cherry Creek belong to this horizon.

In the section at Clarno's Ferry, plants are found at two horizons. The lower one, exposed two or three miles above the Ferry, appears to be the same bed as that cropping out at Cherry Creek. The leaves of the upper horizon were found about one and one-half miles east of the Ferry in a hard shale which weathers to the buff, but is, according to Mr. Calkins, reddish-brown when not exposed. The shales show considerable disturbance and are highly indurated. The Lower John Day resting directly upon them is quite soft and weathers into the mud-covered slopes so characteristic of its outcrops. It seems probable to the writer that the Lower John Day rests unconformably upon these leaf shales.

At Allen's Ranch,[19] on Bridge Creek, leaf beds have been discovered by Condon at the base of the John Day section. The plants occur there in a reddish shale which weathers whitish. Though the writer was unable to find the original locality, he has been assured by Professors Condon and Joseph Le Conte, who visited it together, that the leaf shales belong to a formation which is covered unconformably by the John Day. Mr. F. C. Calkins and Mr. V. C. Osmont, who have collected at this locality, also inclined to the view that these beds are pre-John Day.

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[19] Commonly known as the Bridge Creek locality.

The writer observed typical Lower John Day close to typical Clarno near the original Bridge Creek locality. It would seem that on purely stratigraphic and lithologic grounds the Upper Clarno and the Bridge Creek leaf shales might be considered as the same horizon.

The collections of fossil plants, made by the University expeditions, were all placed in the hands of Professor Knowlton, of the U. S. National Museum, who has kindly furnished the following tentative statement regarding the Clarno flora:—

"It was at first intended to make the present contribution as complete a discussion of the fossil floras of the John Day region as possible, but after working on these collections for a short time it was found that so many changes were necessary, and so many new forms must be characterized, and more especially that other allied floras must be considered, that it would take the paper beyond reasonable limits of size. Hence, it was decided, with the consent of Dr. Merriam, to present here a preliminary and tentative list of the species obtained by him, with such geological conclusions as seem warranted at this time, and reserve the final and complete results for publication in the form of a bulletin of the U. S. Geological Survey. Much of the manuscript for this has already been prepared, but before it can be satisfactorily completed it will be necessary to thoroughly revise all of the late Tertiary floras of the Pacific Coast, more especially the Auriferous Gravels and allied formations of California. It is hoped that this may be ready for publication by the close of the year.

"The collections from Bridge Creek are of considerable size and contain much interesting material, but the collections from most of the other localities are small and fragmentary, consisting in some instances of single specimens only. Following is an enumeration of species arranged according to localities. All new species are indicated by 'n. sp.,' the names and descriptions being reserved for the final publication.

BRIDGE CREEK, Allen's Ranch

[Locality 811]

Sequoia langsdorfii (Brgt.) Heer.
Juglans schimperi Lesq.
Betula angustifolia Newb.
Alnus serrulata fossilis Newb.
Alnus carpinoides Lesq.
Quercus pseudo-alnus Ett.
Quercus consimilis Newb.
Quercus breweri Lesq.
Quercus simplex Newb.
Quercus n. sp.
Quercus sp.
Ulmus n. sp.
Platanus condoni (Newb).
  Ficus? condoni Newb., Proc. U. S. Nat. Mus., Vol. V, p. 512, 1883; Later Extinct Floras, p. 85, pl. LVI, Fig. 1; LVIII, Fig. 1; 1898 [1899].
Platanus aspera Newb.
Platanus sp.
Cratægus flavescens Newb.
  Myrica diversifolia Lesq., Cret. & Tert. Fl., p. 241, pl. L, Fig. 10, 1883.
Grewia ermata Newb.
Fraxinus integrifolia Newb.

ROAD-CROSSING AT CHERRY CREEK

[Locality 804]

Asplenium subsimplex (Lesq.) Kn.
Lygodium kaulfusii Heer.
Equisetum oregonense Newb.
Juglans rugosa Lesq.
Hicoria? n. sp.
Rhamnus cleburni? Lesq.
Fragments.

ONE AND ONE-HALF MILES EAST OF CLARNO'S FERRY

[Locality 832]

Sequoia langsdorfii (Brgt.) Heer.
Alnus corrallina? Lesq.
Alnus carpinoides? Lesq.

Ulmus? sp.
Acer sp.
Fragments.

THREE MILES ABOVE CLARNO'S FERRY

[Locality 840]

Equisetum oregonense Newb.
Zizyphus longifolia? Newb.
Aralia sp.
Aralia?
Fragments.

ONE-HALF MILE NORTHEAST OF FOSSIL

[Locality 844]

Sequoia langsdorfii (Brgt.) Heer.
Alnus carpinoides Lesq.
Myrica? n. sp.
Fragments.

"In attempting to work out the bearing of the plants above enumerated on the question of the age of the beds, it should not be overlooked that any conclusions drawn might be quite different from what they would be were the whole flora of each of the localities to be considered. For example Dr. Merriam's collection from Bridge Creek embraces only fourteen previously named species, whereas the complete known flora of this locality includes over forty species. And further it is impossible at the present time, without having worked out the affinities of the Tertiary floras of California and elsewhere, to give with any degree of completeness the outside relationships of the flora of the John Day region. The following conclusions, however, are not likely to be greatly modified by subsequent work.

"The oldest horizon represented by these collections seems to be that near the crossing of Cherry Creek [loc. 804]. The species though few in number seem to have their greatest affinities with forms from the lower Tertiary, and it is probable that this horizon should be referred to the lower or middle Eocene. There are a few species in common with Bridge Creek but in general its flora has a slightly older facies.

"The Bridge Creek locality [811] as already suggested has an ample flora which is represented by a wealth of individuals. A large proportion of its species are endemic but on considering the obvious relations of these, as well as the forms known from other localities, an upper Eocene age is indicated.

"Several other of the localities seem to be of the same age as the Bridge Creek beds, namely: one and one-half miles east of Clarno's Ferry [loc. 832]; three miles above Clarno's Ferry [loc. 840]; and one-half mile northeast of Fossil [loc. 844]. Not more than three previously-named species are known from either of these localities, and not rarely the identification of some of these is more or less doubtful, but as nearly as can be made out they should be of the same age as Bridge Creek."

It will be noticed that the determination of the plant remains, both as regards the flora as a whole and with respect to its subdivisions, agrees with the statement relating to stratigraphic succession. The Bridge Creek beds, with the few specimens from the shales one and one-half miles east of Clarno's Ferry, are considered upper Eocene, while those from Cherry Creek are held to be an earlier facies.

John Day Series

Resting upon the Clarno formation and extending over the greater portion of the John Day basin, is a thick series of sediments which Marsh[20] called the deposits of the "John Day Lake." It has generally been referred to in geological and palæontological literature as the John Day beds. King[21] correlates this series with his Truckee beds as a part of the deposit of his Pah Ute Lake. In the statement regarding this correlation, King has, however, recognized Marsh's name, so that, if a correlation is attempted, Pah Ute should be displaced by John Day.

General Characters.—Nearly the whole of the John Day formation consists of ashy or tufaceous materials. Only toward the top of the section do we find typical products of erosion. At Haystack, Spray, and in the lower end of Turtle Cove, good exposures show the highest portion of the series to be composed of one or two hundred feet of hard, blocky tuff, below which is about the same thickness of sand and gravel. The gravels are in some places quite coarse, containing pebbles four or five inches in diameter. The sands sometimes show cross-bedding. Included in these deposits are worn fragments of bones and teeth, which probably represent forms similar to those in the beds immediately below.

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[20] O. C. Marsh, Am. Jour. Sc., 1875, 2d ser., Vol. 9, p. 52.

[21] C. King, Survey 40th Parallel, Vol. 1, p. 458.

Rhyolite flows are found toward the lower part of the Middle John Day at Bridge Creek, near the top of this division in Turtle Cove, and overlying what is probably Middle John Day on Pine Creek, about three miles northwest of Spanish Gulch.

The tuffs and ashes seem in some cases to have been worked over somewhat by air or water. At other points, beds many feet thick have apparently been deposited directly, without much, if any, working over by either wind or water.

The source of the ash and tuff is as yet unknown. It probably came from vents not very distant from this basin of deposition.

Excepting the beds of sand and gravel near the top of the section, the stratification throughout the whole thickness of the John Day is very regular. Numerous beds of almost pure ash or tuff compose uniform, hard, and prominent layers, between which in the softer beds the regular deposition of thin layers is plainly indicated by delicate variations in color. Nodular layers, possibly produced in part by contained organic remains, are not infrequent in some localities, and small nodules are usually scattered through a large part of the Middle John Day.

The erosion forms and coloration of the John Day strata are quite characteristic when compared with those of other formations in the basin. In general the beds are colored various shades of red, green, blue, or yellow. In some cases they are white or gray. As will be shown later, the coloration is an important character in distinguishing the subdivisions of the system. The beds are usually quite soft and disintegrate very rapidly, forming a layer of mud several inches thick over a large part of the exposed surface. A moderately heavy rain starts the mud almost in streams, and, as it is soon formed again, erosion must proceed very rapidly. At several localities visited by the writer, groups of unrelated bone fragments, evidently brought together by collectors, were found resting on small pinnacles several inches in height, showing that in ten to twenty years erosion had progressed at least four or five inches in fairly favorable localities.

In the Lower John Day the tendency of erosion is almost always to produce dome-like, mud-covered hills, with scarcely a fragment of the bed-rock protruding anywhere. In the middle division steep, pinnacled bluffs, exhibiting beautifully the typical bad-land structure, are common, and in the uppermost division they are the rule.

Without having accurately measured the John Day section, the writer would not be willing to consider the exposures north of the southern range of mountains as representing a thickness much greater than 2,000 feet. Perhaps it is not more than 1,500 feet thick. At Sheep Rock, near Picture Gorge, the whole section is shown rather sharply tilted, and all but the lower division would be included in the column between the cap rock and the level of the river. At Bridge Creek, also, the section includes the whole of the series. It may reach a thickness somewhat over 2,000 feet at that locality.

Classification on Basis of Lithologic and Stratigraphic Characters. —Owing to the importance of determining the vertical range of the fossil forms contained in this series, it has been desirable to find some marks of recognition, besides purely palæontologic characters, by which the beds of widely-separated sections may be correlated. Though no sharply-defined dividing lines can be drawn inside the series, it is still possible, on the basis of both palæontologic and lithologic characters, to subdivide it into several fairly well-marked divisions.

Wherever the John Day is well exposed in the central and western portion of the basin, it seems to be divisible into three stages, which have been designated[22] the Lower, Middle, and Upper John Day.

The *lower division* consists usually of highly-colored shale, which breaks down readily, forming characteristic mud-covered domes. These beds are in the main a deep red, with occasional alternating strata of buff or white ash. At Bridge Creek alternating beds of red, white, and green, occurring in a group of the typical hills of this division, form a striking feature of the landscape, the colored strata making sharply-defined rings about the hills. At Clarno's Ferry numerous alternations of contorted and faulted, red and white beds are splendidly exposed in prominent hills at the bottom of the section.

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[22] Science, New Series, Feb., 1900, Vol. XI, p. 219.

The beds of this group appear usually to show more deformation than those higher up in the series. This may be due in part to their being softer and having offered less resistance to disturbances than the more rigid strata above them.

The Lower John Day is almost barren of fossil remains at all points where it was visited, and has never, so far as can be discovered, furnished many good specimens. Diligent search by the writer at several localities has been rewarded by the discovery of two or three fragments of rhinoceros teeth. An Oreodon skull was found at this horizon, many years ago, by Mr. L. S. Davis, but definite information regarding it is not now obtainable.

The lower division was estimated to be 250 to 300 feet thick at Clarno's Ferry. Its maximum thickness will probably exceed that limit. It is not impossible that the Lower John Day will sometime be found to be separated by an unconformity from the middle division. Such fossil remains as have so far been found in it indicate, however, that it belongs to the John Day series.

The *middle portion* of the John Day section at Bridge Creek, Clarno's Ferry, and Turtle Cove, consists of drab to bluish-green beds, sometimes forming rounded hills, but more frequently exposed as steep, pinnacled, and ribbed bluffs. Nodular layers and thick beds with small nodules scattered through them are common in this group, while they are rare, if not entirely absent, in the lower division, and are not common in the uppermost beds. The strata of this group are never so sharply contorted as those of the lower division, though they may stand at a fairly high angle and may show considerable faulting.

This stage has probably furnished more fossil remains than the upper division, partly because the remains are here frequently found in hard nodules, which have protected the bones and held them together.

At Bridge Creek a rhyolite flow is interbedded with the lower part of the Middle John Day, or possibly separates it from the lower division. In Turtle Cove a similar flow is found at the top of this division and possibly separates it from the upper group. At many places, particularly in Turtle Cove, hard beds of white to greenish ash and tuff are intercalated between the softer and usually more fossiliferous strata. (See Fig. 2, Pl. 7.)

The middle division is at least 500 feet thick in Turtle Cove, and possibly as much as 800 to 1,000 feet at Bridge Creek.

At most John Day localities, including Bridge Creek, Turtle Cove, and the entire region of the North Fork, the *uppermost beds* in the section are buff, tufaceous, or ashy deposits, sometimes with sand and gravels near the top. These beds show a thickness of at least 300 to 400 feet, and perhaps much more in some localities. They are usually harder and are generally exposed as steeper bluffs than the strata of the lower divisions. The steepness of the bluffs is sometimes partly due to the fact that they are protected by the lavas above, but even where there is no protective covering they tend to assume the same erosion forms.

In the North Fork region, at Monument and Hamilton, red and pinkish beds, resembling the Lower John Day somewhat in color, are found next to and grading into the uppermost division. It is quite certain that some of these exposures at Monument are really Upper John Day, and a close examination shows the rock to be lithologically different from the typical basal shales. At Hamilton a considerable thickness of red beds, looking at a distance much like the typical lower division, was seen to be apparently immediately below the upper beds. It was not possible to examine the exposures and it is not known whether the middle division is missing here or whether the beds are Upper John Day similar to the red phase at Monument.

This division contains the only typical sands and gravels in the John Day and the only known remains of fresh-water mollusca occur here. Excepting a single leaf, the only plant remains known to occur in the series are in the upper division.

While it has not been possible for the writer to draw sharp lines between the divisions discussed, the lithologic characters are in general sufficiently well marked so that one is enabled to determine the horizon in the series to which beds in question belong.

Palæontologic Classification.—That the fauna of the John Day region changed considerably during the period of deposition of this series has already been shown by Wortman[23] who has proposed a division of the series on a palæontological basis into the lower or Diceratherium beds and upper or Merycochœrus beds. Wortman mentions two species of *Merycochœrus*, *Gomphotherium cameloides*, *Elotherium humerosum*, and *Mesohippus præstans*, as characteristic of the upper division, while *Diceratherium* is the typical form of the lower division.

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[23] Extinct Camelidæ of N. America, Bull. Am. Mus., Vol. 10, p. 120.

Dr. W. D. Matthew has recently shown that the John Day Oreodons referred to *Merycochœrus* are generically distinct from Leidy's type. Dr. Matthew has kindly furnished the following note, in which it is shown that these species should be included in a new genus, for which he has proposed the name *Paracotylops*:—

MERYCOCHŒRUS Leidy.	PARACOTYLOPS new genus.	EPOREODON Marsh.
Type *M. proprius* (Leidy).	Type *P.* (*Oreodon*, *Merycochœrus*) *superbus* (Leidy).	Type *E. occidentalis* (Marsh).
Premaxillæ coossified along their entire inner margins.	*Premaxillæ* coossified at tips.	*Premaxillæ* not coossified.
Nasals much reduced.	*Nasals* unreduced.	*Nasals* unreduced.
Infraorbital foramen above m.$^{1-2}$	*Infraorbital foramen* above p.^{4} m.^{1}	*Infraorbital foramen* above p.^{3}
Face suddenly narrowed in front of orbits.	*Face* more gradually narrowed in front of orbits.	*Face* gradually narrowed in front of orbits.
Zygomata greatly expanded.	*Zygomata* greatly or moderately expanded.	*Zygomata* moderately expanded.
Mastoid process greatly expanded into a broad transverse plate.	*Mastoid process* of moderate size.	*Mastoid process* not expanded.
Occiput broad and short, sagittal and transverse crests nearly buried in cellular tissue.	Occiput high and narrow, sagittal and transverse crests very prominent.	Occiput high and narrow, sagittal and transverse crests prominent.
Cellular bony tissue extensively developed on posterior part of skull.	*Little or no cellular bony tissue* on posterior part of skull.	*No cellular bony tissue* on posterior part of skull.
Neck very short.	"Neck rather short" (Scott).	*Neck* of moderate length.

Owing to the change in the name of the characteristic fossil of the Upper John Day, the writer suggests that this division would more appropriately be denominated the Paracotylops beds.

In correspondence regarding the relation of his classification on the basis of faunas to that of the writer, Dr. Wortman states that his Paracotylops (Merycochœrus) beds are doubtless the same as the upper division here proposed, and that his Diceratherium beds would correspond to the middle division. This leaves the lower division without a palæontologic designation, until its fauna shall be discovered. Attention is called in this connection to the fact that in most classifications of the continental Tertiary beds of North America this division is omitted.

The collections made by the University of California parties have been labeled as accurately as possible in the field with reference to horizons, and it is hoped that when the material is finally gotten into form for study it will be possible to obtain more information regarding the vertical distribution of species. Judging from field observations alone, Dr. Wortman would be justified in his classification. The large *Paracotylops* forms were found to be principally, if not entirely, confined to the upper beds, the Oreodons being principally represented by *Eporeodon* in the middle division. Remains of the large Elotheres are most abundant in the buff beds, though they are known also from much lower horizons. Remains of *Gomphotherium*, probably *cameloides*, were found only in the upper division, where they are quite abundant near the junction of the North and South Forks. *Diceratherium* is certainly more abundant in the middle division, though it probably occurs in the highest beds as well.

In a special report on the purely palæontological results of the work of the expedition, this question will receive further consideration.

Extent and Stratigraphic Relations.—The John Day beds are found exposed interruptedly along the John Day River and its tributaries from Clarno's Ferry up to the Picture Gorge, just below Dayville on the South Fork, and probably as far east as Granite Creek on the Middle and North Forks. North of the mountains unmistakable John Day is seen at Fossil and Lone Rock. Exposures near the town of Antelope are possibly also a part of this series. South of the mountains typical deposits are known at Logan Butte near Price.

At Bridge Creek and in Turtle Cove the whole section is exposed. At Clarno's Ferry the lower and middle beds are well shown, and possibly the upper beds in part. About five miles below the ferry lava beds rest directly upon the middle division. Along the main river from Haystack Valley to the junction of the North and South Forks, and from there along the North Fork to Monument, it is principally the upper beds, occasionally with the middle division, that are found. On the Middle Fork the upper beds seem to be the only part of the section present between the pre-Tertiary basement and the lava.

At Fossil several hundred feet of the upper division appear between the Clarno and the Columbia lava. At Lone Rock only the Upper John Day is exposed, though the other divisions may also be present. Mr. V. C. Osmont states that south of the mountains at Logan Butte there is a great thickness of John Day beds, estimated at between 3,000 and 4,000 feet, composed of the upper and middle divisions, with possibly a portion of the lower one. The bottom of the section is not exposed. Though the exposures are not continuous, Mr. Osmont thinks that the beds are pretty certainly not repeated by faulting. Aside from the exposures at Logan Butte, the writer is not aware of the existence of any outcrops of typical John Day south of the Blue Mountains.

The widening of the basin of deposition indicated by greater extent of the upper beds may have been only toward the north, but if the southern section is, as it appears, much thicker than the northern, it is only reasonable to suppose that the basin extended for a considerable distance to the south beyond the farthest point to which it has been traced.

The John Day beds are usually slightly disturbed. They are generally tilted five to ten degrees. From the observations made by the writer, no definite system of folds could be made out, though there seem to be several which trend east and west. Faulting is not uncommon and in some places there has been much friction along the fault planes, so that the soft beds have been changed into hard slate bands several inches in thickness. Both the normal and reverse types of faults are represented. Toward the west end of Haystack Valley a break of unknown extent brings what are probably Middle John Day strata up to the level of the highest beds of the series. At another locality, some miles east of this point, numerous thrusts are beautifully shown in cliff sections. Along the North Fork two systems of fractures were noticed. One trends north and south and the other appears to cross it at nearly a right angle.

As has already been indicated, the series is evidently unconformable upon the Clarno.

In the whole of the region occupied by John Day north of the southern range of the Blue Mountains, it is covered by the Columbian lavas, being accessible only in the deep cañons, where it has been exposed by extensive stream corrosion. At every locality in the basin where the series can be seen, its relations to the overlying formations are beautifully shown. In several places, notably at Sheep Rock in the upper end of Turtle Cove, and on the main river below Spray, residual hills in the middle of the valley are capped by portions of the lower flows, which have served to protect the softer beds beneath.

The Columbia lavas are in some places seen to be decidedly non-conformable to the John Day. Near Haystack the fossil beds form a fairly sharp anticline below lavas which are almost horizontal. At Clarno's Ferry lava flows are seen at one locality to rest upon the middle beds, the typical upper division being absent.

At many points where the contacts of Columbia lava and John Day were examined, fossil wood was found to be abundant. In one place at the lower end of Turtle Cove, where there was much petrified wood at the contact, branches of trees were found pushed up into the lava beds. Some of these stems showed an interesting mode of preservation, being unaltered charcoal on the outside, while the interior was petrified.

Evidently the John Day had been slightly crumpled, had suffered erosion for a considerable period, and was at least partially covered by forest when the first lava floods were poured out.

Mode of Deposition.—The John Day beds have generally been considered as entirely of lacustrine origin, and probably a part of the series has been formed in that way. There are, however, certain peculiarities about a considerable portion of the section which it is difficult to explain by this theory.

As has previously been stated, the John Day is largely made up of volcanic ash and tuff, which does not appear to have suffered much from working over. Sands, gravels, and muds, such as belong to characteristic lake beds, are confined to the top of the series. While molluscan remains are quite common at many horizons, fresh-water forms are known only in the sands and gravels mentioned above. The numerous molluscan shells, found in the ash and tuff beds, are of land forms. Plant remains, also, which characterize lake beds are, excepting some petrified wood, confined to the highest strata. A solitary leaf, found many years ago in the middle stage at Turtle Cove, is the only known exception to this rule. Fish remains have not been found at all in this series. Tortoise bones are very abundant, but so far the writer has not learned of the existence of any water forms of this order. The only aquatic mammalia which have been found are rodents. Remains belonging to members of the beaver family seem to occur at several horizons through the section. In short, while organic remains are abundant in the greater portion of the John Day, aquatic forms are found only in limited sections of the series. One could account for the absence of water forms by supposing the lake to have been salt or alkaline, though there does not appear to be any definite evidence in support of this view.

An objection to the lacustrine hypothesis as applied to the ashy beds is found in the fact that, while the greater part of the deposit is composed of fine material, large, isolated mammalian bones are scattered all through it and over wide areas of the same horizon. Many of these bones are evidently parts of skeletons which were torn apart and scattered about on a land surface before they were finally buried. If they were carried out into a lake it is hard to understand how they could be selected for distribution in deposits from which all other large fragments of detrital material are absent. Occasionally carcasses might be floated out into a lake and finally buried in fine deep-water deposits. In such cases many, if not all, of the bones would be found together. The presence of a considerable portion of the fossil material could not be accounted for in this way.

A possible explanation of these occurrences is that a shallow lake on a wide plain might by expansion and contraction, or shifting its position, ultimately cover and bury bones which had been resting for a long time on the land. The same thing could be accomplished by flowing water in a basin where cutting had largely ceased, or by accumulation of wind-carried dust or ash.

The strongest argument in favor of the lacustrine hypothesis is found in the character of the bedding of the series. The stratification is nearly everywhere absolutely regular and the beds are frequently very thin. Bedding of this kind could be developed only on a floor free from all irregularities. Such deposits, where they are not shown to have accumulated rapidly, are usually considered as having been formed in water.

Recently W. D. Matthew has suggested[24] that the White River beds, which the John Day resembles in a measure, are in part of æolian origin. Except for the regularity and thinness of the bedding, such an hypothesis as this applied to the question of the origin of the John Day would have much in its favor. The material being largely ash, there would be no difficulty in accounting for its origin. If the deposits were formed rapidly enough to prevent dissection, absolute regularity of bedding could be maintained. Here again, however, we meet with a difficulty, as it is hardly probable that a region subjected to frequent ash showers would be inhabited by such numbers of large mammals as would seem to have lived there. If the deposition took place at intervals infrequent enough so that the region could be a desirable place of habitation, it is probable that under ordinary conditions irregularities of the surface would cause noticeable unevenness in the bedding. That the accumulation of the John Day beds occupied a long period is brought out by a study of the vertical distribution of the species, which changed considerably during this epoch.

The thinness of the bedding in places might be urged as an argument against a purely æolian mode of deposition. The writer is not familiar with any æolian deposits that have accumulated slowly, which show thin and well-marked bedding planes.

A theory of fluviatile origin of the series would be open to some of the same objections that have been made to the æolian theory.

A large part of the John Day seems to have been deposited under conditions somewhat different from any that have been generally recognized as governing the accumulation of extensive formations. Other somewhat similar deposits on this side of the continent appear to have been formed in much the same way.

Having originally held to the lacustrine theory of origin for the whole series, it would seem to the writer, after consideration in lights most favorable to this theory of all the evidence obtainable, that, as commonly accepted, it fails to meet fully the necessities of the case for a large part of the section. If it is retained for these beds it will be in some modified form.

The writer would suggest that showers of ash, with tuff deposits, on a plain, occupied perhaps in part by shallow lakes, like the so-called lake-beds of the prairie region of the central plains, might form accumulations similar to those in a large part of the series. If the basin were kept close to base level, irregularities of the surface would hardly be noticeable. Rapid deposition of ash or tuff would occasionally form homogeneous beds of considerable thickness, and would, perhaps, make the region temporarily uninhabitable for most forms of animal or plant life. During the intervals between such periods of rapid deposition, the surface might be partially covered with vegetation and become the home of such animal forms as have left their remains in the fossil beds. The deposition of small quantities of ash during these periods would not necessarily be a hindrance to the occupation of the region by animals or plants, more than the deposition of loess-like dust in the central plains region has prevented its habitation by a complex fauna and flora. Future investigations may show that some of the very thin-bedded portions of the ash deposits were laid down in water, and that the less distinctly stratified beds are largely æolian.

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[24] Am. Naturalist, May, 1899, Vol. 33, p. 403.

Fossil Remains.—The mammalian and molluscan faunas of the John Day are already fairly well known from the numerous contributions to the palæontology of this region by Marsh, Cope, Scott, Wortman, Stearns, and others, and the objects of this paper do not require a further consideration of this subject.

The flora of the John Day was unknown until the summer of 1900, when a small collection of leaves was obtained by the University of California party from the upper beds near Lone Rock. These specimens were examined by Professor Knowlton, who reports upon them as follows:—

"Three and one-half miles south of Lone Rock [locality 861].

Sequoia langsdorfii (Brgt.) Heer.
Juglans n. sp.
Salix sp.
Phyllites n. sp.
Fragments.

"The locality south of Lone Rock [loc. 861] is represented by a single known species. It is impossible to settle the age from these data, but judging from the affinities of certain of the new forms detected this horizon is possibly not far from that of the Van Horn's

Ranch[25] material. Much larger collections must be made before the age can be satisfactorily determined by the plants."

Columbia Lava

The name given to the lava formation above the John Day was first used by I. C. Russell,[26] who applied it to the series of eruptives which forms such a prominent feature of the geology in the area drained by the Columbia River. In the region discussed by Russell there are several distinct horizons of Columbia lava, separated by important formations belonging to different geological periods. Obviously only one of them can retain the name, if it is to be used as a series or formation name in geological classification. This one should be the horizon which is most prominent along the Columbia River, as it was this formation which suggested the name. In the John Day basin it is found that the lavas of the Columbia form a well-defined series which lies between the John Day and the Mascall formations. Other eruptives in this region are hardly to be confused with it. This series is, moreover, that one of the several to which the name is applied which has the greatest lateral extent, forming probably the largest lava field of the world and one of the most important formations on this continent. It would seem advisable to restrict the name Columbia lava to this horizon.

The lava series is composed of a large number of basalt flows which are sometimes separated by beds of tuff. At Turtle Cove twenty-three flows were counted in the bluff. Nowhere does it seem to be less than 1,000 feet thick, and it would average much above that over the greater part of the basin.

Though no attempt was made to trace out any of the flows, it was noted that some of them seem to extend for many miles.

A hint as to the mode of exit of the lava is furnished by the occurrence of basaltic dikes in the John Day beds at many localities. The largest and most important of those that have come to the writer's notice are the Davis dikes, which run in nearly a straight line, with few if any breaks, for about fifteen miles through the lower end of Turtle Cove and out into the valley of the main river. The dike shows transverse columnar structure at most points. At the only place where its thickness was estimated, it was about twelve feet in diameter, but it certainly reaches several times that width along a good part of its course.

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[25] Mascall formation.

[26] Bull. No. 108 U. S. Geol. Survey, p. 20.

In most places where the contact of dikes with the fossil beds was observed, the bounding walls seem to have suffered little, if any, change. At one point, however, on the west side of Turtle Cove, where the Davis dikes cut the Upper John Day, a most interesting contact phenomenon is noticeable. The ashy fossil beds here exhibit a most remarkable development of columnar structure for a distance of about fifteen feet from the lava on each side. The columns are approximately normal to the surface of the dike and fairly straight. The faces are very even, the columns being as regular and sharply cut as the most perfect structures developed in basalt. The dike at this point is multiple, and portions of the fossil beds caught between the leaves have also developed columnar structure, with this exception, that the columns are there much larger than those bounding the dike on the outside. The outer columns are noticeably small, averaging about two inches in diameter, even when ten or more feet in length; while some of those developed in a band of John Day deposit about two feet thick, caught in the midst of the dike, show a diameter of about five inches. Evidently the greater heat and slower cooling tended to increase the size of the columns.

As far east as the writer's observations extend, viz., to Dale on the north and Mt. Vernon on the south, the Columbia lava has formerly covered the whole country. There do not appear to have been any islands in this sea of stone. Over most of this region the lava beds still remain fairly flat. They are rarely inclined more than five or ten degrees.

Along the north side of the East Fork Valley from Mt. Vernon to Picture Gorge, and from there westerly toward Caleb, the Columbia lavas are inclined sharply to the south. Along the valley they pass beneath the river and below the Mascall formation. At Picture Gorge, where the lavas are cut through by the river, they show a dip of about twenty degrees or more to the south. On the south side of this valley the southern range of the Blue Mountains is capped with Columbia lava. In the Crooked River region the lavas appear again beneath the Mascall formation.

Viewing the East Fork Valley from near Caleb it is quite evident that the Columbia lavas are sharply faulted or bent along its south side, the downthrow being to the north. Near the western end of the valley a number of nearly vertical beds are exposed high up on the southern slope. Persons who have visited these outcrops inform me that they are lava, and I have supposed them to be beds dragged down along the plane of a fault or sharp fold. In the depression to the north of the fault plane there rest several post-Columbia lava formations which, as will be shown later, have also been affected by this disturbance.

Mascall Formation

Nomenclature.—Along the valley of the East Fork and south of the Blue Mountains, there is found, resting upon the Columbia lava, a series of sediments which have been known in the literature as the Cottonwood[27] beds, the Loup Fork[28] beds, the Ticholeptus[29] beds (in part), and the Amyzon[30] beds. Recently Wortman has placed his palæontological horizon known as the Protolabis[31] beds in this formation. None of these names appear to be applicable to the formation considered as a stratigraphic unit. The term Cottonwood is pre-occupied, having been used for a carboniferous formation by Prof. C. S. Prosser. It is very doubtful whether it can ever be shown that this series and the true Loup Fork occupy the same horizon in the standard geological scale. As yet it has not been done. The Ticholeptus beds probably belong to another horizon than the one with which we are dealing. The correlation of this series with the Amyzon beds was due to its confusion with the Clarno at Bridge Creek. Wortman's Protolabis beds will doubtless be found to cover a considerable portion of this formation, but as the section is perhaps a thousand feet or more in thickness it is most probable that it will be found to represent more than one palæontological horizon. It is, moreover, advisable to separate palæontological horizon names from those used for formations or stratigraphic units. It is, therefore, proposed to designate these beds as the Mascall formation. The typical exposure is near the Mascall Ranch, four miles below Dayville.

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[27] Bull. Am. Mus. Nat. Hist., Vol. XII, p. 23, also Jour. Geol., Vol. IX, p. 72.

[28] Manual of Geology, 4th Ed., J. D. Dana, p. 895.

[29] E. D. Cope, Am. Nat., 1886, Vol. 20, p. 367.

[30] E. D. Cope, Proc. Am. Phil. Soc., 1880, Vol. 19, p. 61.

[31] J. L. Wortman, Bull. Am. Mus. Nat. Hist., Vol. X, pp. 120, 141.

Occurrence and Stratigraphic Relations.—In the valley of the East Fork the Mascall formation rests in the depression formed by the deflexed Columbia lavas. (See Fig. 1.) The dip of the lower beds is here approximately the same as that of the lava beds below them; the uppermost strata may be slightly flatter. On Birch Creek and at several other localities, there is some evidence of intercalation of lava flows between the lower strata. The Mascall beds do not reach to the level of the lava plateau to the north, though they may formerly have passed over it. They have suffered much erosion and a later formation rests upon their worn edges. So far, the writer has learned of no deposits corresponding to the Mascall in the northern part of the basin. The Ellensburg beds of central Washington, described by Russell,[32] are probably in part of the same age, but may have accumulated in a different basin.

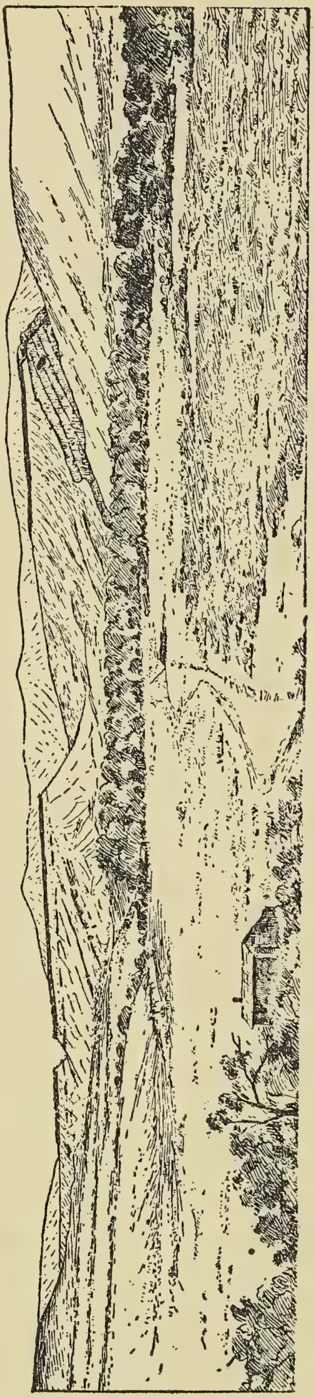

Fig. 1. Sketch of John Day Valley between Picture Gorge and Dayville. Gorge cut in Columbia lava. Mascall formation resting on lava and covered by Rattlesnake beds.

At Rattlesnake Creek near Cottonwood the Mascall is not less than 800 to 1,000 feet thick. The beds are made up largely of ash and tuff and are generally light colored, though there are some brownish and reddish strata. Coarse detrital materials are generally absent from the typical section on the north side of the East Fork Valley.

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[32] Bull. 108, U. S. Geol. Surv., p. 22, also 20th Ann. Rep., U. S. Geol. Surv., Part II, p. 127.

Six miles above Dayville there are exposed along the south side of the valley about 400–500 feet of conglomerate, sand, ash, and tuff, forming a syncline pitching to the southeast. The steepest dip seen in the main section here is about 30°, but at the foot of the bluff there are some exposures of gravel beds which are nearly vertical. Pebbles from several horizons in this section were examined, but none seemed to be derived from the Columbia lava. Two other exposures of gravel were seen some miles west of this point, also on the south side of the river. Whether these beds are upper Mascall or whether they belong in some other formation is not clear to the writer. Fragmentary leaf remains were found about the middle of the section, and sufficient material could possibly be obtained there to throw some light upon the age of the horizon.

Fossil Remains.—The Mascall formation has furnished many fossil remains, including those of mammals, testudinates, fish, and plants. The vertebrate fossils are neither so numerous nor so well preserved as those in the John Day. Teeth and single bones comprise the greater part of most collections made here. The mammalian remains show the fauna to have been of a much more specialized and higher type than that of the John Day.

Fish remains are found associated with plants in the lower part of the formation near the old Van Horn ranch. The single species known from this locality has been referred by Cope[33] to the genus *Plioplarchus*, a member of the perch family.

Plant remains are very abundant in the shales at Van Horn's Ranch and other localities near the bottom of the section. The collection made here by Captain Bendire was studied by Professor Lesquereux, who considered it upper Miocene. A collection made by the University party in 1900 was submitted to Prof. F. H. Knowlton, who has furnished the following list, with a statement regarding the probable horizon to which the flora belongs:—

"Van Horn's Ranch, about half way between Cañon City and Dayville on East Fork. [Locality 878.]

Glyptostrobus ungeri Heer.
Taxodium distichum miocenum Heer.

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[33] Am. Nat., 1889, Vol. 23, p. 625.

Idnyites sp.
Salix angusta Al. Br.
Quercus pseudo-lyrata Lesq.
  Quercus pseudo-lyrata acutiloba Lesq., Proc. U. S. Nat. Mus., vol. xi, p. 17, pl. xi, fig. 1, 1888.
  Quercus pseudo-lyrata brevifolia Lesq., op. cit., p. 18, pl. x, fig. 2, 1888.
  Quercus pseudo-lyrata latifolia Lesq., op. cit., p. 18, pl. xii, fig. 1, 1888.
  Quercus pseudo-lyrata obtusiloba Lesq., op. cit., p. 18, pl. x, fig. 3, 1888.
Quercus n. sp.
Quercus n. sp.
Quercus? sp.
Planua ungeri Ett.
Ficus? oregoniana Lesq.
Laurus n. sp.
Aralia whitneyi? Lesq.
Acer bendirei Lesq.
Acer dimorphum Lesq.
Acer n. sp.
Sapindus obtusifolius Lesq.
Prunus n. sp.
Prunus n. sp.
Hydrangea bendirei (Ward).
  Marsilea Bendirei Ward, Sketch of Paleobotany, 5th Ann. Rept. U. S. Geol. Surv., p. 446, 1883–84.
  Povana Bendirei (Ward) Lesq., Proc. U. S. Nat. Mus., vol. xi, p. 16, pl. viii, fig. 4, 1888.

"Gravel and tuff section, south side of East Fork Valley. Four miles east of Dayville. [Locality 880.]

Carpinus grandis Unger.

"The flora of Van Horn Ranch [loc. 878] finds its greatest affinity with the Auriferous gravels and allied floras of California and is to be regarded as upper Miocene in age.

"The locality four miles east of Dayville [loc. 880] is represented by a single species. A larger collection from this locality will be needed before the age can be satisfactorily determined by the plants."

It is the plant and fish horizon of the lower Mascall which Cope referred to the Amyzon beds. It was apparently supposed to have the same relation to the John Day as the Clarno leaf beds at Bridge Creek.

Origin.—The numerous remains of plants and fish in the fine white beds at Van Horn Ranch indicate lacustrine conditions at this locality during the early portion of the period. Similar leaf beds in the Crooked River region which have been described to the writer possibly originated in the same way and at or near the same time.

In the upper part of the section at Cottonwood, the conditions of deposition, so far as can be ascertained, seem to have been similar to those under which the John Day was laid down. Should the gravels on the south side of the East Fork valley prove to be the uppermost beds of the Mascall formation, the era of deposition would appear to be concluded in a manner similar to that in which the John Day ended.

Rattlesnake Formation

Throughout the length of the Mascall formation exposures in the valley of the East Fork, they are seen everywhere to have been capped at one time by a series of later deposits which have sometimes been confused with them. To these beds the name Rattlesnake formation is applied by the writer, the typical occurrence being on Rattlesnake Creek about one mile west of Cottonwood. The Rattlesnake has been referred to by Wortman and Matthew[34] as the "gravels" at the top of the Cottonwood section. Possibly Cope also refers to them in an indirect way, though the writer is not able to determine certainly just what is meant by his statement.

Stratigraphy.—In Fig. 2, Pl. 8, and Fig. 1, p. 470, the typical exposures of the Rattlesnake show it resting unconformably upon the Mascall. It is usually inclined only slightly, having a southerly dip of about five degrees. At one locality on Birch Creek where a section of the Rattlesnake was carefully examined, it was found to comprise 30–40 feet of coarse basal gravels, above this about 25 feet of soft brown tuff, and capping this about 30 feet of rhyolite. At other localities more than 100 feet of gravel have been seen upon the rhyolite. The basal gravel beds show a thickness of 200 feet or more in other localities. They are frequently very coarse and contain many pebbles evidently derived from the Columbia lava.

In the Birch Creek section the base of the rhyolite flow is filled

[34] W. D. Matthew, Bull. Am. Mus., Vol. 12, p. 23.

with angular pebbles of Columbia lava. A stratum about one foot thick at the bottom is largely made up of pebbles, and above that, at least half way up to the top of the flow, pebbles are found scattered through the mass. The rhyolite exhibits everywhere a tendency to split up into large irregular columns about twenty-five feet across. At several localities near the mouth of Beach Creek, a radial or bouquet-like columnar structure is beautifully developed in it. The columns are here about 12–15 inches in diameter. They are sharply separated from each other and show remarkable regularity. The rhyolite extends as a very uniform flow for at least fifty miles westward from Mt. Vernon. It is said by Mr. Osmont to reach up the valley at least 15 miles above Cañon City. Osmont also states that it caps the Mascall formation in the Crooked River region. Being much more resistant than the underlying beds, it has tended to form broad tables or terraces wherever it occurs.

Fossils.—The Rattlesnake gravels contain many vertebrate remains, most of which have heretofore been listed with the Mascall fauna. The Rattlesnake fossils when weathered out are frequently to be found resting upon the Mascall beds below, and as most of the material from both Rattlesnake and Mascall is found detached from the matrix, the difficulties in the way of separating the faunas are considerable. So far no segregated lists of the species have been published.

Basin of Deposition.—The floor upon which the Rattlesnake was laid down consisted largely of the upturned and eroded Mascall beds. The basin of deposition was bounded on the north by a range of hills formed by the upper portion of the Columbia lava monocline. At the present time the northern limits of the basin may be clearly seen, as large portions of the deposit have escaped erosion and extend along the northern side of the East Fork valley and westward to the divide some miles beyond Caleb. These considerable remnants all fall into a nearly horizontal plane which abuts against the lava hills to the north. Looking out over the Rattlesnake table-lands from Spanish Gulch one can see an almost continuous series of these deposits, which are in nearly their original position and have not suffered greatly from erosion. It requires no great effort for one to picture to one's self this part of the basin in its original form.

Deformation.—At Picture Gorge, on the north side of the valley, the Rattlesnake rhyolite extends to within a few yards of the Columbia lava and would rest upon it if the section were not interrupted by the gorge. On the south side of the valley it is not well represented, and, where present, is frequently much broken up. The southerly inclination of this bed and its broken character on the south side of the valley indicate that considerable movement has taken place in post-Rattlesnake time along the plane of the fault which has broken the Columbia lava at this point. This movement is a continuation of that which had given the Mascall formation a southerly dip before the Rattlesnake was deposited upon it.

South of the Blue Mountains, according to Osmont, the rhyolite flow appears again in its typical form and rests upon the Mascall formation.

The present drainage of the John Day must have been established before the tilting of the Rattlesnake took place, as the river now turns sharply to the north at Picture Gorge, leaving the soft deposits of Mascall and Rattlesnake, which extend farther to the west in the direction which the stream has run for many miles, and cutting straight through the Columbia lava monocline. Had the movement taken place before the cutting of this gap was initiated, the river would probably have been thrown toward the southern side of the valley and would never have come out at this point.

Age of the Rattlesnake.—Without making any attempt at exact correlation of the Rattlesnake with any other formation, there seems to be sufficient evidence to show that it should be considered as belonging to the Pliocene of the standard scale; perhaps it represents only the later portion of that period. Its stratigraphic relations to the Mascall formation are such that it could not be older than early or middle Pliocene, while the amount of erosion which took place between the close of this epoch and the middle or latter part of the Quaternary shows that it could not possibly be later than Pliocene.

QUATERNARY

Terraces.—At numerous points along the John Day and its tributaries, one or more terraces are to be found not far above the existing floor of the valley. At the upper end of Haystack Valley on the main John Day, gravels containing numerous large rounded pebbles of rocks not outcropping in that neighborhood are exposed on a terrace about 75–100 feet above the river. Twenty-five feet below this is the sagebrush flat made up of alluvium with numerous angular boulders and pebbles from the hills near by. At another locality, about two miles farther up the river, water-worn gravels were again seen on well-marked benches.

Along a considerable part of the river, terraces representing parts of ancient alluvial fans or slopes are very common. On the north side of Bridge Creek near Allen's Ranch numerous broad, gently-sloping tables separated by gullies sometimes several hundred feet deep represent an old and very regular alluvial slope. The stream cuttings here show in places a considerable thickness of the John Day beds capped by irregularly stratified wash from the adjacent lava bluffs.

In terrace deposits remains of *Elephas* and *Equus* have been found at several localities. Near Mt. Vernon, on the East Fork, a nearly complete skeleton of *Elephas primigenius* was discovered in an alluvial deposit not much above the level of the river. Whether or not the other remains have been worked over from older deposits, this skeleton has evidently not been disturbed.

Cañon Cutting.—The discovery of typical Quaternary forms in deposits so near the valley floor shows that the cañon cutting had been practically finished for some time when Quaternary mammals were still in this region. In other words, the period of active cañon-cutting did not extend to the close of the Quaternary. The backward extension of this period is limited by the Rattlesnake. Though the drainage was probably established before the close of that epoch, the great work of corrasion was accomplished after the river began cutting into the uppermost Rattlesnake beds. A palæontological determination of the age of the Rattlesnake would very materially aid in fixing more exactly the probable earlier limit of the era of cañon-cutting. The greatest probable extension of this epoch is from late Pliocene to middle Quaternary. On these broad lines a correlation of this period with the Sierran[35] epoch of Le Conte would seem to be justified.

Ash Beds.—At many localities, particularly in the northern part of the John Day basin, an ash bed of comparatively recent origin is seen in the flood plain deposits or on the alluvial slopes near the streams. In the upper end of Haystack Valley a stratum about 1½ feet thick is exposed at several places in the river bank. It is here covered by 6–10 feet of alluvium with angular pebbles. On Rudio Creek there are fine exposures of an ash bed along the bank of the stream. The bed is here much thicker than at Haystack. Similar deposits were seen as far east as the writer has explored.

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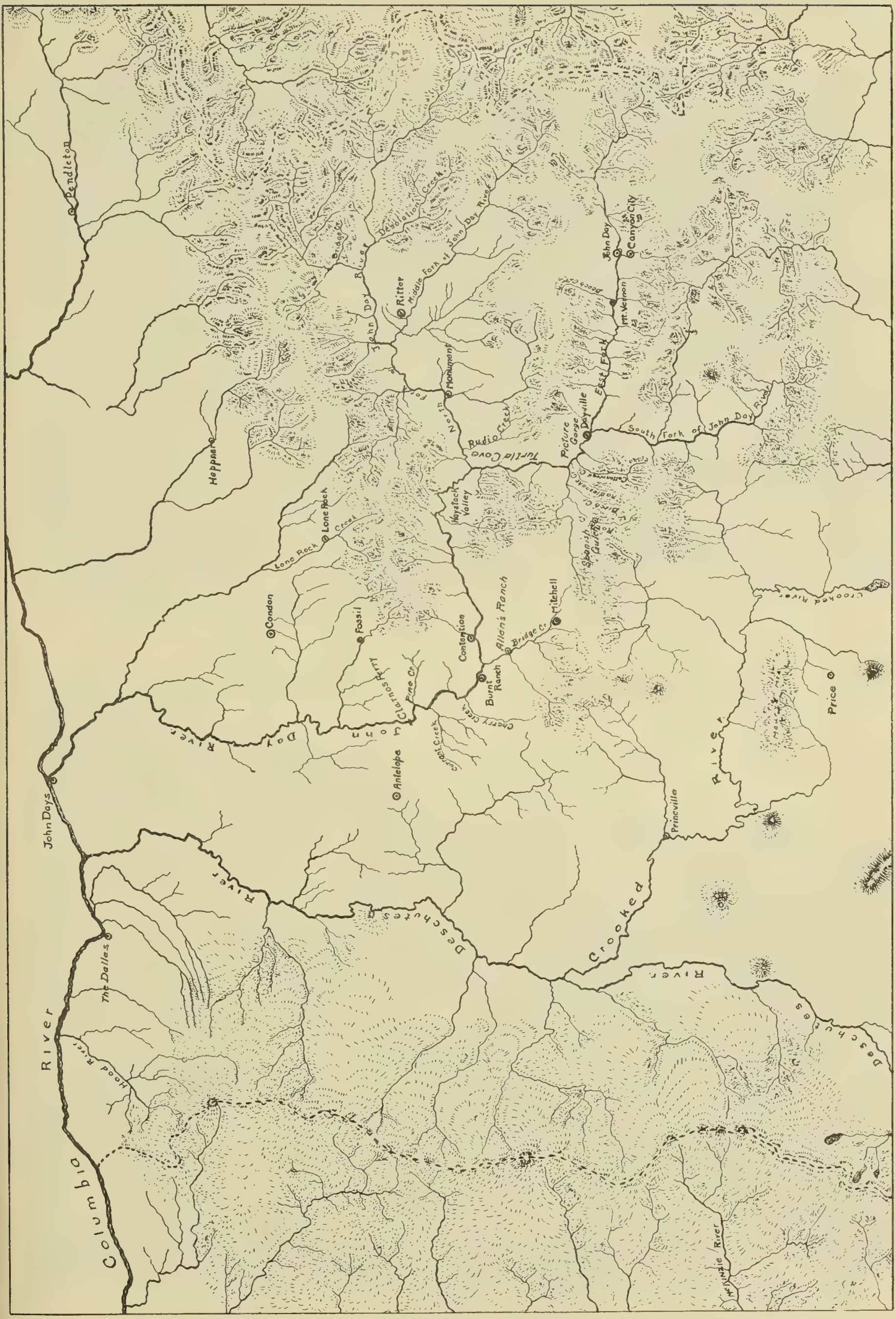
[35] Jour. Geol., 1899, Vol. 7, p. 525.

Though deposits somewhat similar to those described might be formed by material washed down from fossil beds or other deposits of volcanic materials, the origin of these beds can not be ascribed to such a cause. Where they have been carefully examined the ash is perfectly pure and is sharply separated from the deposits above and below. It has apparently not been worked over appreciably and was probably deposited rapidly, otherwise it would be mingled with other detrital material. Its deposition is evidently to be correlated with some catastrophic volcanic outburst occurring in comparatively recent times. Possibly it has been derived from the volcanoes of the Cascade Range.

University of California
April, 1901


Pendleton
Heppner
Bridge Cr.
Desolation Creek
Middle Fork of John Day River
John Day River
Ritter
Monument
North Fork
Rudio Creek
Turtle Cove
Picture Gorge
Dayville
East Fork
Mt. Vernon
John Day
Canyon City
Beech Cr.
South Fork of John Day River
Haystack Valley
Spanish Gulch
Lone Rock
Lone Rock Creek
Condon
Fossil
Clarnos Ferry
Pine Cr.
Contention
Allen's Ranch
Bridge Cr.
Mitchell
Burnt Ranch
Cherry Creek
Currant Creek
Antelope
John Day River
Crooked River
Price
Princeville
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Deschutes River
Deschutes River
John Days
The Dalles
Columbia River
Hood River
McKenzie River

Sketch map of north central Oregon. 1 inch = 32 miles

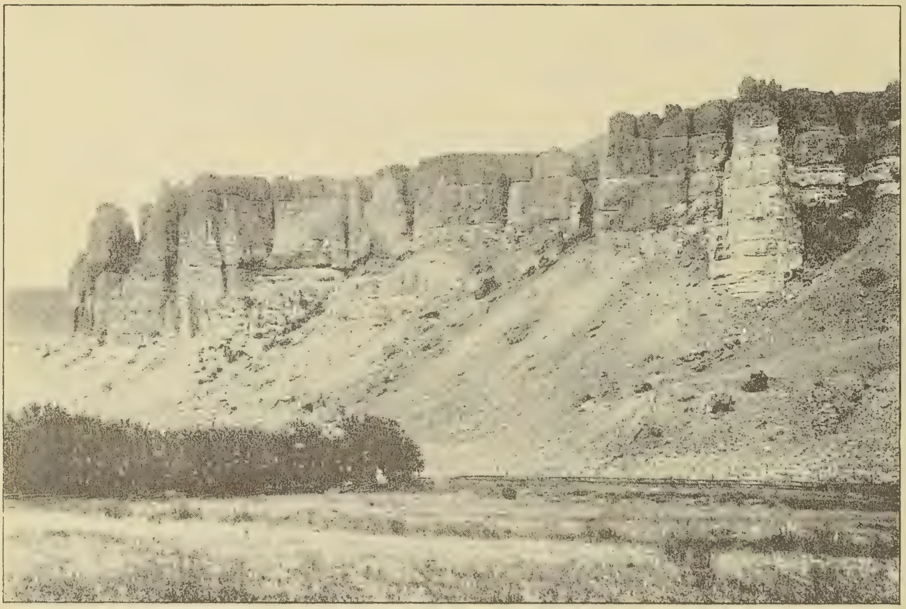

FIG. 1. Typical exposure of Clarno formation, Pine Creek, near Clarno's Ferry.

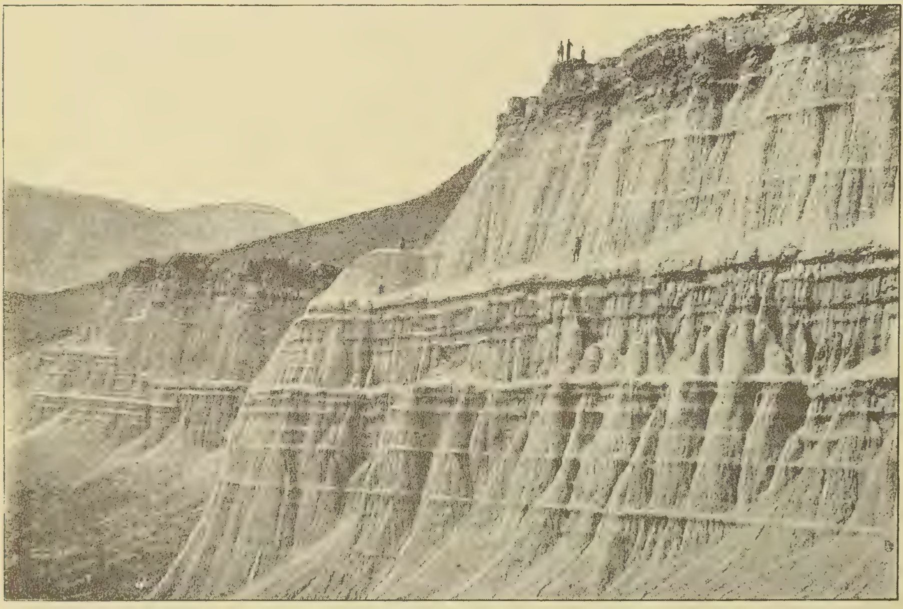

FIG. 2. Typical exposure of Middle John Day, Turtle Cove.

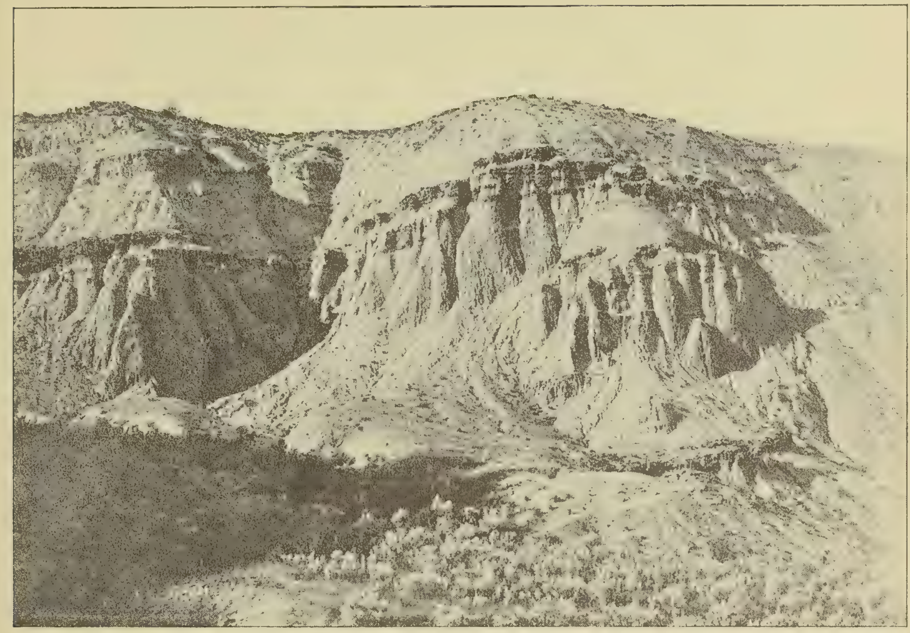

FIG. 1. Upper John Day, Haystack Valley, showing sands and gravel. Erosion forms not particularly characteristic of this horizon.

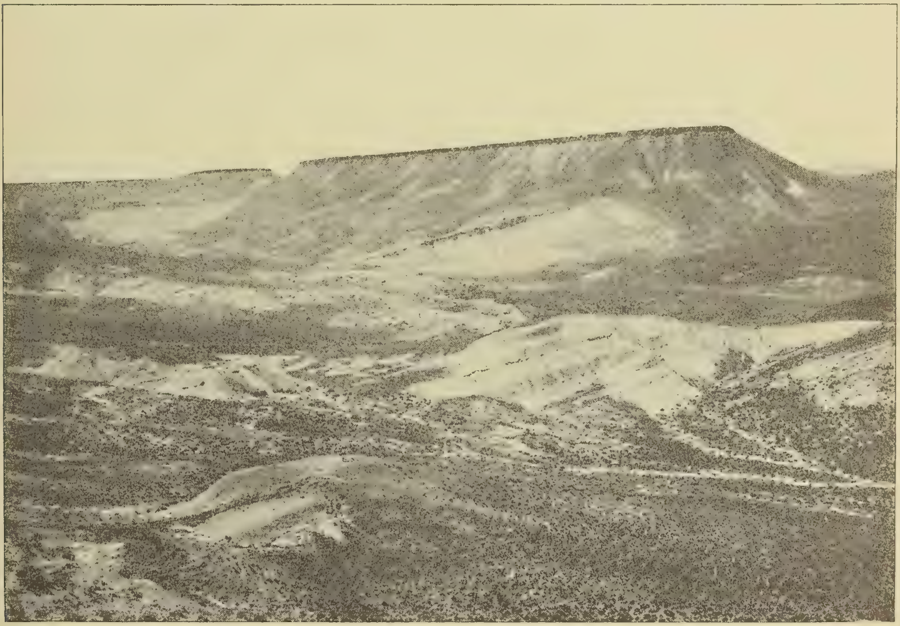

FIG. 2. Mascall formation with unconformably overlying Rattlesnake beds, near mouth of Rattlesnake Creek.

CARNIVORA FROM THE TERTIARY FORMATIONS OF THE JOHN DAY REGION

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INTRODUCTION

In 1899 and 1900 field parties from the University of California, working under the direction of the writer, collected over the greater part of the exposed area of the Tertiary formations in the John Day Valley of Eastern Oregon. In the fall of 1900 L. S. Davis and V. C. Osmont continued in the field after the University party had returned, and made additional collections, particularly in

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the region of the Crooked River and Logan Butte, south of the John Day Basin. The collections of Osmont and Davis were purchased for the University, and the material now available may be considered representative of all the phases of the faunas of the John Day region. The new rodent and ungulate material from these collections has already been discussed by Dr. Sinclair.[1] In the following paper there are presented such additions to our knowledge of this fauna as have been obtained from a study of the carnivore material.

In the preparation of this report the writer has been especially indebted to Professor H. F. Osborn and Dr. W. D. Matthew of the American Museum for courtesies extended during the examination of the Cope collection of John Day types. Dr. Matthew has also very kindly made numerous examinations of types for me while the material was in the process of description. Professor W. B. Scott and Dr. Marcus Farr have shown me the types of John Day Carnivora at Princeton University, and Dr. Sinclair has recently reexamined several types at my request.

In working over the subject of variation in the dentition and skull characters of the recent Canidae, Dr. C. Hart Merriam and Mr. Vernon Bailey have furnished most valuable data. In the examination of the Canidae, Mr. Bailey has worked over a very large series of skulls and has reported on over fifteen hundred examinations.

In justice to the artist and engraver, it should be stated that the illustrations accompanying this paper were reproduced from the first rough proofs, the original plates and drawings having been destroyed in the San Francisco fire of April eighteenth.

OCCURRENCE

The general stratigraphic succession of the Tertiary formations of the John Day region has been discussed by the writer in a previous paper.[2] The sequence of formations recognized is as follows:—

John Day River terraces	Quaternary
Rattlesnake formation	Pliocene
Mascall formation	Miocene
Columbia Lava formation	Miocene

[1] W. J. Sinclair. Bull. Dept. Geol., Univ. Cal., Vol. 4, No. 6.

[2] Bull. Dept. Geol., Univ. Cal., Vol. 2, No. 9.

John Day series	Miocene to Oligocene
Upper John Day	
Middle John Day	
Lower John Day	
Clarno formation	Eocene
Upper Clarno	
Lower Clarno	

Of these formations, those included in the beds below the Pliocene are made up mainly of igneous materials. The John Day and Mascall beds are almost entirely composed of volcanic ash and tuff in various forms. Mammal remains are known from the John Day, Mascall, Rattlesnake, and Terrace deposits.

Excepting the uppermost portion of the series, the John Day beds show a remarkable evenness in their stratification, and contain a fauna which is characteristic of dry land. In the higher strata, cross-bedding appears, with more or less interstratified gravel, and a number of fresh-water types are seen in the fauna. The greater portion of the series is presumably made up of slow accumulations of ash, which fell mainly on open plains, upon which shifting shallow lakes may have existed from time to time. In the the latter portion of this period the topography appears to have been more diversified and the action of streams to have become more pronounced.

The greater portion of the total thickness of the Mascall is, like the John Day, made up of evenly stratified ash beds. In the lower portion of the formation there is, however, evidence of accumulation of a considerable thickness of fine sediment in a body of fresh water. In this there are numerous remains of fresh-water fishes and mollusks, and large quantities of fossil plants.

The Rattlesnake beds consist mainly of heavy gravels. Associated with these, as a very prominent and persistent feature, is a heavy rhyolite flow. Some of the beds beneath the rhyolite evidently represent old alluvial floors which have been built up largely by dust accumulations.

Although the Carnivora of the Tertiary faunas of the John Day region have been known through numerous types, the actual number of specimens is not large, and they may be counted as among the rarities. It is interesting to note that in the collections obtained by the University of California, there is a considerable percentage of new forms, although the number of specimens is relatively small. This indicates that the fauna is still only imperfectly represented in the collections. As yet, carnivore remains are certainly known only from the John Day and Mascall.

As far as possible in our field work, the effort has been made to determine the stratigraphic horizons in which specimens have been found. While the results of this discrimination have been most apparent in the study of the Ungulata, some light has also been thrown on the history of the Carnivora. Of the known carnivore species from this region there are still a considerable number of which the geological range or occurrence is unknown. As far as has been determined, the following are the time relations of the species. The number of specimens known to occur at each horizon is indicated by the figures in the table.

	Middle John Day	Upper John Day	Mascall
Canis (*?*) sp.	...	...	1(?)
Tephrocyon rurestris	...	...	1
Cynodictis (*?*) *oregonensis*	2	...	...
Nothocyon geismarianus mollis	1	...	...
Nothocyon lemur	3	3(?)	...
Nothocyon latidens (*?*)	2	...	...
Mesocyon coryphaeus	2	5	...
Mesocyon brachyops	...	1(?)	...
Mesocyon josephi (*?*)	1	...	...
Temnocyon altigenis	2	1(?)	...
Temnocyon ferox	...	1	...
Philotrox condoni	1	...	...
Archaelurus debilis major	7	...	...
Nimravus gomphodus	1	...	...
Pogonodon davisi	...	1	...
Pogonodon platycopis	1	...	...

CANIDAE

The Tertiary beds of eastern Oregon have furnished a remarkable variety of canid types compared with other formations in America. Nearly all of these are known from the John Day beds, only two of the eighteen species occurring in the Mascall. Although most of the types represented exhibit some primitive characters, much variation in structure is shown. In some cases the differentiation has led to development of considerably specialized forms. In the following discussion only those species have been touched upon, concerning which additional evidence has been obtained.

The following are the recognized species occurring in the John Day and Mascall:—

MASCALL
- *Canis* (?) *sp.*
- *Tephrocyon rurestris* Condon.

JOHN DAY
- *Paradaphaenus cuspigerus* Cope.
- *Cynodictis* (?) *oregonensis*, n. sp.
- *Nothocyon geismarianus* Cope.
- *Nothocyon lemur* Cope.
- *Nothocyon latidens* Cope.
- *Mesocyon coryphaeus* Cope.
- *Mesocyon brachyops*, n. sp.
- *Mesocyon josephi* Cope.
- *Temnocyon altigenis* Cope.
- *Temnocyon wallovianus* Cope.
- *Temnocyon ferox* Eyerman.
- *Philotrox condoni*, n. gen. and sp.
- *Oligobunis crassivultus* Cope.
- *Enhydrocyon stenocephalus* Cope.
- *Hyaenocyon basilatus* Cope.
- *Hyaenocyon sectorius* Cope.

CANIS (?) sp.

Text-figure 1

The known material representing this species consists of two well-preserved upper molars in a fragment of a jaw. The teeth resemble those of the coyotes in general form, and are tentatively referred to the genus *Canis*. They are a little smaller than the molars of the living coyotes in this region, and M^2 is relatively a little larger.

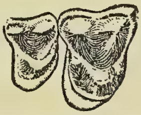

FIG. 1. *Canis* sp. No. 545. Mascall beds (?), Rattlesnake Creek, near Cottonwood, Wheeler County, Oregon. × 1.

The outer cusps of M^1 are laterally compressed and rather sharp. The protocone is well developed, but the inner cusp of the cingulum is relatively small. The intermediate tubercles are both present. The outer ridge of the cingulum is well defined, but is narrow.

On M^2 the metacone is about as large as the paracone. The V-shaped protocone is distinct and the inner cusp or hypocone is well developed.

Measurements

	mm.
M^1, greatest antero-posterior diameter	9.7
M^1, greatest transverse diameter	13.3
M^2, greatest antero-posterior diameter	6.6
M^2, greatest transverse diameter	9.8

The only known specimen, No. 545, was obtained between Cottonwood Creek and Birch Creek, in the southeast corner of Wheeler County, Oregon. (Locality No. 887, Univ. Calif. Coll. Vert. Palae.) At this locality the Mascall formation is capped by the Rattlesnake beds. This specimen was obtained on an exposure of Mascall beds immediately below a Rattlesnake outcrop. It was not in the matrix, and we cannot be absolutely certain that it had not originally come from the Rattlesnake beds above.

TEPHROCYON, New Genus

TEPHROCYON RURESTRIS Condon

Pl. 1, Figs. 1, 2, and 3

Canis rurestris Condon, The Two Islands, 1902, p. 139, Pl. 18. Type specimen No. 382, private collection of Professor Thomas Condon.

This species is represented by a very fine skull obtained by Professor Thomas Condon many years ago in the Mascall formation near Cottonwood, Grant County, Oregon. It was figured by Professor Condon in his work on the Two Islands and was afterward kindly loaned to the author by him for comparison and study. The skull lacks only the portion anterior to the canines. The parts present are well preserved and in good condition for study.

Distinctive Characters.—Muzzle short, posterior ends of premaxillaries extending behind the anterior ends of the frontals, sagittal crest high, inion prominent, auditory bullae very large, inferior margin of the mandible strongly convex below the anterior side of the coronoid process. Dentition $\frac{3}{3}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{2}{3}$. P^4 with incipient protostyle, deuterocone weak. M^1 with broad internal lobe, apparently without protoconule. P_2, P_3, and P_4 with posterior basal tubercles and without anterior cusps. M_1 with well-developed metaconid, heel with low entoconid and hypoconid. Trigonid of M_2 with distinct paraconid. M_3 with three or four low tubercles or ridges.

Skull.—The type of skull shown in this species is that of a short-muzzled form with greatly developed temporal muscles. The shortening of the facial region is accompanied by relatively great backward extension of the premaxillaries, which pass the anterior ends of the frontals, and almost reach a line connecting the anterior borders of the orbits.

The sagittal crest is high and sharp. The inion projects rather more than is typical of *Canis*. The occipital region shows strong buttresses running out on either side to the lambdoidal crest. The auditory bullae are very large, and the paroccipital processes prominent.

On the mandible, the massateric fossa is deep. The inferior margin of the jaw shows a somewhat greater degree of convexity below the anterior end of the massateric fossa than is common in the typical canids.

Dentition.—The dentition is in general much like that of *Canis*, but differs in the presence of a notch on the anterior side of P^4, which separates an incipient protostyle from the protocone; in the presence of a minute paraconid on M_2, and of several tubercles on M_3; and in the greater width of the lingual side of M^1.

All the premolars excepting the first are represented in both jaws. The presence of the anterior one is indicated in both cases by a large alveolus. P_2, P_3, and P_4 have no anterior cusps or tubercles, but all exhibit both a posterior cusp and posterior basal tubercle. P^2 differs from all of the other premolars, excepting the carnassial, in possessing a minute anterior cusp. P^3 shows both a posterior cusp and a posterior basal tubercle. On the upper carnassial, a distinct notch on the anterior side of the protocone separates a small cusp corresponding to the protostyle. The deuterocone is small.

The first upper molar is unusually broad on the lingual side, though the posterior inner cusp or hypocone is not relatively large. A well-developed metaconule is present, but there is apparently no protoconule. The external cingulum is distinctly marked. On M^2 the protocone is large and the metacone somewhat reduced.

M_1 is not far from the stage of evolution seen in *Canis*, though the metaconid is perhaps a little larger in *Tephrocyon*. On the heel the low hypoconid and entoconid are distinctly separated. The trigonid of M_2 is less reduced than in *Canis*, and possesses a small paraconid. The heel of this tooth is not markedly different from that of *Canis*. The hypoconid is a distinct but low tubercle.

On M_3 there is a faint external ridge with three smaller ridges running toward the inner margin. These elevations seem to represent the hypoconid and the three elements of the trigonid.

Affinities.—This form seems to be generically separable from the canids thus far described from the Miocene of America, but it shows affinities with *Canis*, and to a certain extent with *Aelurodon*.

In the Canidae, the development of a protostyle on P^4 is a characteristic of the Aelurodons and *Simocyon*, though occurring occasionally in other forms. In its incipient form it is present rarely in modern species of *Canis*, particularly in the milk carnassial. In order to determine the degree of variability existing in wild canid species, Dr. C. Hart Merriam and Mr. Vernon Bailey have recently examined a large series of skulls in the collections of the Biological Survey. The following results I quote from a statement by Dr. Merriam.

"In the big Wolf, out of 107 skulls, a faint trace of a cusp may be seen in 1 adult.

"In Coyotes, out of 450 skulls, a faint trace exists in 3 adults, and a distinct cusp is present in the milk tooth of 15 young.

"In *Canis* (or *Cerdocyon*) *magellanicus*, out of 22 skulls, no trace of a cusp in the adult; a faint cusp is present in the milk tooth of 2 out of 6 young.

"In Red Foxes, out of 244 skulls, no trace in adult; slight trace in milk tooth of 5 out of 10 young.

"In Kit and Desert Foxes, out of 70 skulls, 2 adults show trace of a cusp; 9 young have a small cusp on the milk tooth in each case.

"In the Arctic Fox, out of 24 skulls, 1 adult shows a faint trace, and 5 young in milk teeth show a faint trace.

"In *Urocyon*, out of 241 skulls, 2 adults and 3 young in milk teeth show trace of a cusp; other young show no trace.

"It is probably an exaggeration to state that any of the adults show a trace of the real protostyle."

The cusp as it appears in *T. rurestris* is stronger than in any variation of the recent *Canis* which I have seen, but it is much weaker than in *Aelurodon*, and should hardly be termed a true protostyle. This species also shows some resemblance to the Aelurodons in M^1 and M_2. It is distinguished from *Aelurodon*, among other characters, by the very imperfect development of the protostyle of P^4, the less reduced metaconid of M_1, the larger M^2, and the large inner lobe of M^1. In most of the characters in which it differs from *Aelurodon*, it approaches *Canis*.

Tephrocyon differs from *Canis* in the structure of P^4, M_2, and M_3, as indicated in the discussion of the dentition above. There are also differences in the skull. The premaxillaries pass the anterior ends of the frontals, the sagittal crest is very prominent, the otic bullae are extraordinarily large, and the mandible is strongly convex below the posterior molars.

The genus is more primitive than the typical Aelurodons in the imperfect development of the protostyle of P^4, and in the larger metaconid of M_1. It is more primitive than *Canis* in the characters of M_2 and M_3. The anterior molars in both jaws are near the stage of evolution seen in *Canis*. As the animal was a rather large form with short facial region and heavy-bladed carnassials, it was probably a rapidly specializing form. The trend of its specialization seems to have been toward the *Aelurodon* type.

Aelurodon was represented by several species in the Loup Fork epoch, but I am not aware of the existence of any remains from older beds. The Mascall beds have been thought to represent a somewhat earlier epoch than the typical Loup Fork, and it is at precisely this horizon that we would search for the ancestral type of the *Aelurodon* group. While it is not necessarily true that *Tephrocyon rurestris* is directly ancestral to *Aelurodon*, it seems to represent a tendency toward specialization in that direction in the Canidae, at the time when the genus *Aelurodon* probably had its origin, and it is evidently not far removed from this line of descent.

MEASUREMENTS

	mm.
Length, anterior end of orbit to inion	124
Length, postorbital process to inion	97
Width between orbits	38
Width across snout above middle of superior canine	38
Length of mandible from anterior side of P_1 to posterior side of condyle	108
Height of mandible below protocone of M_1	20

	mm.
Length, anterior side of P^1 to posterior side of M^2	60
Length, anterior side of P$_1$ to posterior side of M$_3$	66
Antero-posterior diameter of superior canine at base	10
P^2, antero-posterior diameter	8.5
P^3, antero-posterior diameter	10
P^4, antero-posterior diameter	17
P^4, greatest transverse diameter	9.5
M^1, antero-posterior diameter	13
M^1, greatest transverse diameter	16
M^1, antero-posterior diameter across protocone	10
M^2, antero-posterior diameter	7.7
M^2, greatest transverse diameter	12
P$_2$, antero-posterior diameter	7.5
P$_3$, antero-posterior diameter	9
P$_4$, antero-posterior diameter	11.5
M$_1$, antero-posterior diameter	20
M$_1$, antero-posterior diameter of heel	6
M$_2$, antero-posterior diameter	11.5
M$_2$, antero-posterior diameter of heel	4
M$_3$, antero-posterior diameter	5

CYNODICTIS (?) OREGONENSIS, n. sp.

Pl. 2, Figs. 4 and 5

Canis gregarius Cope, Bull. U. S. Geol. Surv. Terrs., 1879, p. 58.
Galecynus gregarius Cope, Tertiary Vertebrata, p. 917, Pl. 68, Figs. 5 to 8.

The specific name *oregonensis* is here applied to the John Day representatives of *Cynodictis* (*?*) (*Galecynus*) *gregarius* Cope. The John Day form has generally passed under the same name as the species from the White River. It is to be distinguished from the latter by the constant presence of a posterior cusp in addition to the anterior and posterior basal tubercles on P$_2$, the larger M^2, larger brain case, less pronounced postorbital constriction, and other characters.[3] Scott[4] has already pointed out that "the John Day specimens, which Cope has referred to *Cynodictis gregarius*, have an even fuller cranium and shallower postorbital constriction, which should, perhaps, be reason for separating these animals specifically from the White River forms."

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[3] In recent correspondence regarding comparisons of specimens at the American Museum, Dr. W. D. Matthew has added the following to the above mentioned characters, distinguishing this form from *C. gregarius*: "Skull wider; muzzle somewhat wider; interorbital width somewhat greater; premolars and carnassials slightly smaller; M^1 more quadrate internally, the hypocone crescent extending farther forward around the protocone; M$_2$ much larger."

[4] W. B. Scott. Canidae of the White River Oligocene, p. 368.

This species is represented in our collections by several specimens. The most important of these is a mandible (No. 316, pl. 2, fig. 4) showing the dentition excepting the median incisors, P_1, and M_3. In addition to this there is a jaw fragment with the unworn M_1 and P_4, and several fragmentary mandibles. A fragment of a maxillary (No. 1179) with both molars perfectly preserved may also belong here.

In the specimens which have come under my observation the characters mentioned above are constant. Compared with the other species of the John Day fauna, the lower sectorial is also diagnostic. The dimensions of the tooth are near those of specimen No. 10256, discussed below with *N. latidens*. It is distinguished from this form by the absence of the postero-external tubercle on the base of the protoconid, by the more distinctly basin-shaped talon, and by the absence or weak development of the external cingulum, excepting a faint ridge below the paraconid. The hypoconid and entoconid are sharply compressed ridges connected posteriorly, while in the form represented by No. 10256 the entoconid is smaller, is nearly conical and is not so closely connected with the hypoconid. On M_2 there is a small but acute paraconid. Although smaller than the other tubercles of the trigonid, it is nevertheless distinctly developed. The enamel of most of the premolars and molars is strongly wrinkled.

It seems not improbable that the lower jaws referred to *Galecynus lemur* by Cope really belonged in *C.* (*?*) *oregonensis*. None of the specimens described by him were in association with crania. The dimensions of his specimens are almost identical with those of *oregonensis*. As indicated elsewhere,[5] there is some reason to believe that a number of the very small inferior sectorials showing the peculiar characters of *latidens* really represent *lemur*.

MEASUREMENTS

	No. 316	No. 365	No. 584
Length of mandible, anterior side canine to posterior side P_4	23.8 mm.		
Height of mandible below protoconid of M_1	8		
P_2, antero-posterior diameter	4.5		
P_4, antero-posterior diameter	6.2	5.9	7
M_1, antero-posterior diameter	8.2	7.9	10.5
M_1, antero-posterior diameter of heel	2.7	2.7	3.6

[5] See p. 493, this paper.

A skull fragment (No. 584, see measurements above) showing a perfect inferior sectorial with P_3, P_4, the trigonid of M_1, and a part of the first upper molar represents an animal considerably larger than the typical *C.* (*?*) *oregonensis.* The form of the teeth is much the same as in *oregonensis* and is quite different from that in *latidens* and *geismarianus.* I think it is very doubtful whether this form belongs in *oregonensis,* but the amount of variation shown in all the groups of John Day dogs is so great that I hesitate to separate it until more is known concerning it.

NOTHOCYON GEISMARIANUS Cope, n. var. MOLLIS

Pl. 2, Fig. 1, and Pl. 3, Fig. 1

Type specimen No. 90, Univ. Calif. Col. Vert. Palae. From the Middle John Day Beds at Turtle Cove, John Day River, Oregon.

A perfectly preserved cranium with dentition represents a type differing somewhat from the other small canids of the John Day. The skull is that of an adult animal with somewhat worn teeth. It is much larger than the skull of *lemur* and considerably smaller than the typical *geismarianus.* The brain case is large and the facial region short. The orbits are smaller than in *lemur,* while the auditory bullae are relatively as large as in that species. The cranium is rather sharply constricted behind the acute postorbital processes. The temporal ridges show a lyrate arrangement, though it is not so strongly marked as in *lemur.* The ridges are separated by a space from 9 to 12 mm. wide, excepting over the posterior portion of the brain case, where they unite to form a low crest about 15 mm. in front of the inion. The dentition represents a stage between that of *Cynodictis* (*?*) *oregonensis* and *N. latidens.* P^3 seems to have had a posterior cusp, though the posterior margin is worn and only a trace of the cusp is preserved. The superior carnassial and the molars are of the broad type, but are narrower than in *latidens.* Except for the somewhat smaller size, lyrate arrangement of the temporal ridges and somewhat narrower molars, this form is close to *N. geismarianus.* It differs from *C.* (*?*) *oregonensis* in its larger size, larger brain case, much larger otic bullae, longer lyrate temporal area, and broader teeth.

This specimen represents a variation of the *Nothocyon* type which cannot be placed in any of the described species without apparently extending the limits of the group so far as to overlap some other species. The uniting of any of the types now known does not seem advisable until more is known of intermediate stages. Neither does it seem desirable to increase the number of species where considerable variation is suggested. I have therefore referred to this form as a variant of the *geismarianus* type. Later investigations may show that it should be raised to specific rank.

Approaching *Cynodictis* (?) *oregonensis* rather closely, as it does, this form makes a separation of the John Day *Cynodictis* type from the more specialized *Nothocyon* very difficult, if it is really possible.

MEASUREMENTS

	mm.
Length, premaxillary to inion	104
Length, postorbital process of frontal to inion	54
Length of superior dental series	50
P^3, antero-posterior diameter	6.2
P^4, antero-posterior diameter	9
P^4, transverse diameter across deuterocone	5.2
M^1, antero-posterior diameter	7.4
M^1, transverse diameter	9.2
M^2, antero-posterior diameter	4.6
M^2, transverse diameter	7.2
Long diameter of otic bulla	19
Width between otic bullae	7
Elevation of inion above foramen magnum	16
Width between canines	12.5
Length of superior dental series including canine	44

NOTHOCYON LEMUR Cope

Pl. 2, Figs. 2, 3, and 8

Galecynus lemur Cope, Bull. U. S. Geol. Surv., v. 6, p. 181, and Tertiary Vertebrata, p. 931.

Cynodictis lemur (Scott), Trans. Amer. Phil. Soc., 1898, p. 400.

Nothocyon lemur (Wortman and Matthew), Bull. Am. Mus. Nat. Hist., v. 12, p. 127.

This species is represented by two crania, by several upper jaws with well-preserved teeth, and by a number of loose molars. Several lower sectorials and jaws discussed under the next species possibly belong here also. Although no mandibles have as yet been found in association with crania, there seems to be some reason for believing that the inferior dentition of *lemur* is much like that of *latidens*, as is indicated in the discussion of *latidens* following.

The following measurements of upper teeth of several individuals of the *lemur* type show considerable variation, but all point toward this species rather than *latidens*.

MEASUREMENTS

	N. latidens Type	*N. lemur* Type[6]	*lemur* Cotype Cope[7]	No. $\overline{56}$	No. $\overline{15}$	No. $\overline{352}$
P^4, antero-posterior diameter	7	7	7	7.2	...	...
M^1, antero-posterior diameter	7	5	5.8	5.8	5.3	5.3
M^1, transverse diameter	8	7.8	7.8	7.4	7.4	7..
M^2, antero-posterior diameter	4.5	3.8	3.5	3.6	...	...
M^2, transverse diameter	5	5.2	5	5.25	...	...

In a small cranium (pl. 2, fig. 2, No. 10208) having the general form and dimensions of *lemur*, the snout is exceedingly narrow, the temporal ridges do not unite posteriorly and the brain case is relatively very large. It appears even larger than in *lemur*, and the superior outline is strongly convex over the parietals.

Another small, narrow-nosed skull evidently belonging in *lemur* exhibits a perfectly preserved brain cast (pl. 2, fig. 3, No. 10209) illustrating the principal features of both cerebrum and cerebellum. This specimen resembles *lemur* in dimensions and general form. In most respects the brain of this species is strongly similar to that of *Cynodictis* as figured by Scott[8] for *C. gregarius* of the White River.

NOTHOCYON LATIDENS Cope

Pl. 2, Figs. 6 and 7

Galecynus latidens Cope, Bull. U. S. Geol. Surv., Vol. 6, p. 181, 1881.
Cynodictis latidens (Scott), Trans. Am. Phil. Soc., 1898, p. 400.
Nothocyon latidens (Wortman and Matthew), Bull. Am. Mus. Nat. Hist., Vol. 12, p. 127.

In our collection there is a perfectly preserved and unworn inferior carnassial (pl. 2, figs. 6 and 7, No. 88) exhibiting a feature which Cope considered characteristic of *latidens*, *viz.*, the "possession of a narrow tubercle at the external base of the principal cusp." There is also a very small tubercle anterior to the base of the entoconid. The length of this tooth is somewhat less than that of the type of *latidens*, and the heel is relatively short. In another specimen (No. 10256) consisting of a large portion of a lower jaw with P_4 and M_1, the external tubercle at the base of the protoconid and the smaller one anterior to the entoconid are both present. The external tubercle is, however, greatly reduced by wear without the remainder of the tooth appearing much worn. The dimensions of this jaw and of the heel of M_1 are considerably less than those of the type of *latidens*, and are nearer the dimensions required by *lemur*. These relations together with the fact that the jaws described as *lemur* agree with *Cynodictis* (*?*) *oregonensis* seem to indicate that the small sectorials just described possibly belong to *lemur*, and that the presence of the external tubercle on the base of the protoconid is a characteristic of *lemur* as well as of *latidens*.

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[6] No. 6888, Amer. Mus. Nat. Hist., Col. Vert. Palae.

[7] No. 6889, Amer. Mus. Nat. Hist., Col. Vert. Palae.

[8] W. B. Scott. Canidae of the White River Oligocene, 1898. Trans. Am. Phil. Soc., Vol. 19, Pl. 19, Fig. 12.

MEASUREMENTS

	No. 10256	No. 88	Type spec. *latidens*	Type spec. *lemur*
P_4, antero-posterior diameter	6	...	5.5	...
M_1, antero-posterior diameter	8.2	7.6	8	8
M_1, antero-posterior diameter of heel	2.8	2.8	3.5	[9]3
Depth of ramus at sectorial	8	...	10.5	8

MESOCYON CORYPHAEUS Cope

Temnocyon coryphaeus Cope, Proc. Philad. Acad., 1879, p. 180; and Tertiary Vertebrata, p. 906.

Mesocyon coryphaeus (Scott), Princeton College Bull. 2, No. 2, p. 38, Apr., 1890.

Hypotemnodon coryphaeus (Eyerman), Am. Geol., Vol. 14, p. 321, 1894.

This species is represented in the collection by several crania and mandibles. Specimen No. 1383 shows the complete upper dentition, of which particularly the sectorial and the molars are unworn and in perfect state of preservation. In No. 1165 the upper dentition is complete excepting the incisors. Both of these specimens agree with Cope's type very closely in their measurements. Another cranium (No. 1692) representing the genus *Mesocyon* differs from both *M. coryphaeus* and *M. josephi*, and has been made the type of a new species described below.

A well-preserved mandible (No. 1307) shows the type of dentition in *M. coryphaeus*. The sectorials are somewhat worn, so that no internal tubercle is shown. The tuberculars are very imperfectly preserved. On another specimen (No. 10366) the last two premolars, the sectorial, and the first tubercular are perfectly preserved. The measurements of these jaws, as also of several detached teeth, are considerably less than those of the type of *M. coryphaeus*, as is indicated in the measurements below. Although Cope states that the mandible described by him was associated with the smallest of the several skulls available, I find that the dentition of mandible No. 1307 in our collection fits the dentition of the skulls of *coryphaeus*, particularly that of No. 1165, very closely, and seems also to have the dimensions required for the mandible of the type cranium. The measurements available seem to indicate considerable variation in size among the forms of this group.

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[9] According to Cope's figure, Tert. Vert., Pl. 70, Fig. 7*a*.

MEASUREMENTS[10]

	Type	No. 1307	No. 599	No. 10366
M_1, antero-posterior diameter	18	16.5	15	14.5
M_2, antero-posterior diameter	....	....	...	7.3
P_4, antero-posterior diameter	11	10	...	10.5
P_3, antero-posterior diameter	....	9.4	...	8.7
Height of jaw below protoconid of M_1	19.3	17	...	18
Height of jaw below protoconid of P_2	....	15	...	....

MESOCYON BRACHYOPS, n. sp.

Text-figure 2

Type specimen No. 1692, Univ. Cal. Col. Vert. Pal. From the upper portion of the John Day series at Logan Butte, Crook County, Oregon.

Facial region and palate relatively shorter than in either *M. coryphaeus* or *M. josephi*. Superior dental series somewhat crowded anteriorly, so that P^1 is very close to the canine. Superior sectorial and first tubercular with dimensions near those of *coryphaeus*, and absolutely larger than in *josephi*. The brain case is relatively larger than in *coryphaeus*.

This is evidently a true *Mesocyon* near the *coryphaeus* type, possessing like that form both posterior cusp and basal tubercle on P^3. The sectorial is nearly as large as in *coryphaeus*. P^3 and

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[10] See also measurements of superior dental series of *coryphaeus* below, p. 496.

P^2 are relatively smaller. The palate is as wide posteriorly as in *coryphaeus*, and the width between the canines is also as great, but the palate of the typical *coryphaeus* is 15 to 20 per cent. longer. There is a moderate degree of crowding of the premolars anteriorly, in contrast to the open arrangement in *coryphaeus* and *josephi*. The size of the brain case is relatively considerably greater than in the type of *coryphaeus* or in a specimen of the same general dimensions in our collection. *M. josephi* differs from this form in having a longer palate, a smaller superior sectorial and first molar, and in lacking a posterior cusp on P^3.

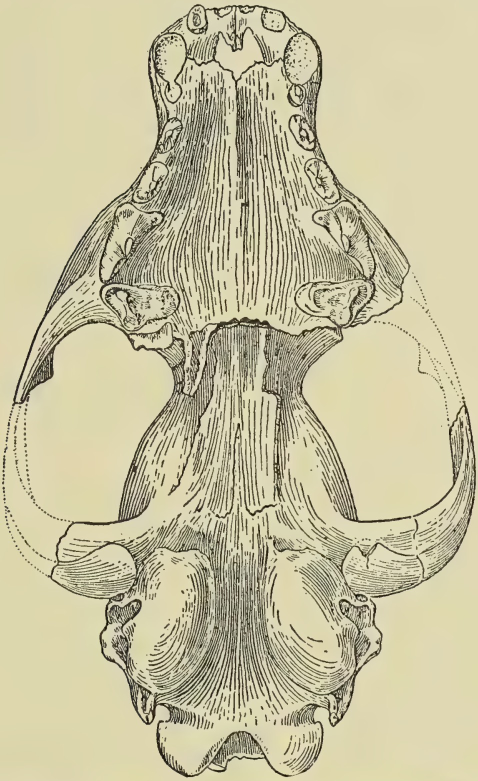

FIG. 2. *Mesocyon brachyops*, n. sp. No. 1692. John Day beds, Logan Butte, Crook County, Oregon. × ½.

The presence of this short-faced variety in close association with long-faced forms of the same group is another illustration of the interesting tendency toward the evolution of short-faced forms in the John Day.

MEASUREMENTS

	M. josephi type	*M. brachyops* type, No. $\overline{1692}$	*M. coryphaeus* type	*M. coryphaeus* No. $\overline{1165}$	*M. coryphaeus* No. $\overline{1383}$
Length, premaxillary to occipital condyle inclusive	....	134	160	....	.....
Length, posterior side of C to posterior side of M^1	47*[11]	43.4	50*	*a*51	53
Antero-posterior diameter of canine	....	9	11*	....	.....
P^1, antero-posterior diameter	3.8*	4.1	4.5*	4.1	4.6
P^2, antero-posterior diameter	8.7*	7	8.5*	8.4	9.+
P^3, antero-posterior diameter	9	8.4	9.5	9.6	10.+
P^4, antero-posterior diameter	12.5	14.2	15	13.6	14.2
P^4, transverse diameter across deuterocone	7	8.3	9*	8.4	8.6
M^1, antero-posterior diameter	8	8.5	9*	9	9.8
M^1, transverse diameter	11	14.3	15*	*a*13.4	15.3
M^2, antero-posterior diameter	4		4.3*	5	5.2
M^2, transverse diameter	7.5		8*	9	9.7
Width of palate between deuterocones of sectorials		26	26.5*	....	.....
Width between canines	....	17	17	....	.....
Length postorbital process to inion		74	86*	....	.....
Greatest transverse diameter of brain case	....	43.5	45*	....	.....
Greatest height of brain case above meatus auditorius	....	32	32*	....	.....

a Approximate.

MESOCYON JOSEPHI Cope (?)

Temnocyon josephi Cope, Bull. U. S. Geol. Surv. Terrs., Vol. 6, p. 179; and Tertiary Vertebrata, p. 912.

Hypotemnodon josephi (Wortman and Matthew), Bull. Am. Mus. Nat. Hist., Vol. 12, p. 130.

Mesocyon josephi (Hay), Bull. U. S. Geol. Survey, No. 179, p. 773.

A mandible somewhat smaller than the lower jaw of *M. coryphaeus* figured by Cope is not far from the size required for the jaw of *M. josephi*, and may represent that species. This specimen (No. 364) shows distinctly the structure of P_2, which has not been described in *Mesocyon*. This tooth has both anterior and posterior basal tubercles in addition to a well-developed posterior cusp. The heel of the sectorial, although slightly damaged, seems to differ from that of the typical *Mesocyon coryphaeus*. The hypoconid is somewhat smaller and lower, and the entoconid is relatively larger, the type of heel being as well adapted to crushing as to cutting. M_2 and M_3 are represented only by the roots and alveoli. They both appear to have been relatively large teeth, and M_3 had two roots instead of one as in *coryphaeus*. If this is *M. josephi* there may be reason to believe that this species is a characteristic form of the Middle John Day, while the larger *coryphaeus* seems to have been common in the Upper John Day, though possibly present in the middle division also.

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[11] In the absence of other data, these measurements are taken from Cope's figures of the type (*op. cit.*, Pls. 70 and 71), and will probably be found to differ slightly from the exact measurements of the specimen.

MEASUREMENTS

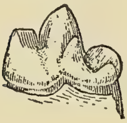
	mm.
M_1, antero-posterior diameter	15.5
P_4, antero-posterior diameter	8.8
P_2, antero-posterior diameter	7
Height of jaw below protoconid of M_1	16
Height of jaw below protoconid of P_2	15

INDETERMINATE

Text-figures 4, 5, and 6

Several loose teeth, which have not been connected with determinable specimens, show peculiar characters of the inferior molars not recognized as yet in any of the John Day canids. In text-figure 4 there is shown the heel of a M_2 and a perfect M_3 preserved in a jaw fragment (No. 672) found at the same locality in the Middle John Day beds with specimen No. 364 tentatively referred above to *M. josephi*. In this specimen the entoconid and hypoconid of M_2 are both well developed. M_3 is a broad tooth with a large talon. The small protoconid and the metaconid are very close together, and the paraconid shelf is much reduced. The entoconid and hypoconid are larger and farther apart than the tubercles of the trigon. In *Mesocyon coryphaeus* the talon of M_2 supports a single tubercle. The second and third inferior molars of *M. josephi* are unknown, though one might suspect from the character of the specimen described above that they are broader than in *M. coryphaeus*. The heel of M_2 in *Philotrox condoni* is broader than in *M. coryphaeus*, but does not show a development of the entoconid and hypoconid comparable to that seen here. The form of M_2 in *Oligobunis* appears to be quite different from that in this specimen, and M_3 is absent. M_2 is said to be trenchant in *Enhydrocyon* and is unknown in *Hyaenocyon*.

Another peculiar specimen (No. 1516), text-figures 5 and 6, representing a portion of an inferior sectorial with a well-preserved heel, was found in the Upper John Day beds at the lower end of Turtle Cove. It shows a hypoconid and an entoconid of almost exactly equal size. It is distinguished from the sectorial of the jaw tentatively referred to *M. josephi* by the presence of a distinctly marked basal band on the outer side of the talonid. This tooth differs from all of the John Day canids with which I am acquainted. It may represent a *Mesocyon* or possibly one of the short-jawed forms.



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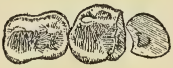

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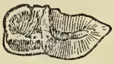

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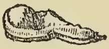

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FIG. 3. *Mesocyon coryphaeus* Cope. Inner side of right M_1. No. 599. Upper portion of John Day Series, Haystack Valley, John Day River, Oregon. × 1.

FIG. 4. Indeterminate. Superior aspect of left M_2 and M_3. No. 672. Middle John Day, below Clarno's Ferry, John Day River, Oregon. × 1½.

FIG. 5. Indeterminate. Superior aspect of right M_1. No. 1516. Upper John Day, Turtle Cove, John Day Valley, Oregon. × 1.

FIG. 6. Outer side of M_1 shown in fig. 5. × 1.

TEMNOCYON ALTIGENIS Cope

Pl. 3, Fig. 2, and Text-figures 7, 8, 9, 10, and 11

Temnocyon altigenis Cope, Palaeont. Bull. No. 30, p. 6, 1878; Rep. U. S. Geol. Surv. Terrs., Vol. 3, p. 903, Pl. 68, Fig. 9, 9*a*, 9*b*, Pl. 70, Fig. 11.

This species, constituting the type of the genus *Temnocyon*, has been only partially known, and was considered by Cope as one of the rarer John Day carnivores. It is represented in the University collections by two specimens, No. 9999, a young adult with unworn teeth, and 1549, an old individual with teeth considerably worn. No. 9999 shows the entire skull with the complete upper and lower dentition, and the greater part of the skeleton excepting the manus and the distal half of the pes. The other specimen is a nearly complete cranium with all the elements of the upper dentition. The dentition of the mandible in the first specimen corresponds very closely to that of Cope's type. The upper dentition is nearer in form to that of Cope's type of *altigenis* as figured than to any other species, with the exception of the deuterocone of the carnassial. In this tooth our specimens exhibit the heavy form of deuterocone seen in the type of *T. ferox*. In Cope's specimen showing the upper jaw, the deuterocone of P^4, though prominent, is represented as small, low, narrow, and not very sharply separated from the protocone. Although this cranium was not associated with the type, the molars show so close a resemblance to those of specimen No. 9999 that there seemed to be good reason for believing that the deuterocone of P^4 had not been correctly drawn. Dr. W. D. Matthew has very kindly examined Cope's type of the cranium for me recently to ascertain the true character of this tooth, and finds that "the upper fourth premolar has a large, well separated deuterocone." The molars of this specimen were found by Dr. Matthew to be correctly represented. With this correction of the original description of *Temnocyon altigenis*, specimens No. 1549 and No. 9999 approach this species very closely. The principal difference being found in minor variations of the measurements as seen in the table of measurements on page 505. Both of the specimens used as types by Cope are slightly larger than the specimens in our collection.

The differences separating this species from the other members of the genus *Temnocyon* may be expressed as follows:—

T. ferox Eyerman. Largest known species. Length of skull in type specimen 266 mm. Sagittal crest high. Deuterocone of P^4 large and heavy, sharply separated from protocone, with an incipient tubercle on the anterior side. P^3 with posterior basal tubercle. M^1 with V-shaped protocone. M^2 with greatly reduced metacone. P_4 practically equaling M_1 in length, with a distinct posterior basal tubercle in addition to the prominent cusp arising from the posterior side of the protoconid.

T. altigenis Cope. Species of medium size. Length of skull 178 mm. in No. 9999, somewhat greater in No. 1549. P_4 heavy and wide anteriorly; deuterocone very large and heavy, separated from protocone by deep valley, without anterior conule. P^3 without posterior basal tubercle. Protocone of M^1 nearly conical, regularly rounded posteriorly but with a short antero-external ridge. M^2 with metacone smaller than paracone, but considerably larger than in the other species. P_4 considerably shorter antero-posteriorly than M_1, with prominent cusp on posterior side of protoconid and with incipient posterior basal tubercle.

T. wallovianus Cope. Species of medium size. Deuterocone of P^4 apparently not greatly enlarged. P^3 without posterior basal tubercle. M^2 small, with reduced metacone. This species should possibly be included in *T. altigenis*.

The principal features of the skeleton of *T. altigenis* as shown in specimens 9999 and 1549 mainly confirm the generic characters represented in the specimen of *T. ferox* described by Eyerman. In some cases, however, the specific differences are great enough to modify slightly our estimate of the generic characters based on the description of *ferox*.

Skull.—The skull of *T. altigenis* differs considerably from that of *ferox* in general outlines. As represented by Eyerman,[12] the cranium of *ferox* is relatively high and narrow compared with the undistorted specimen of *altigenis* seen in No. 1549. A part of this difference may be due to lateral crushing in the *ferox* specimen, which would produce the deviation in height and width at the same time. The palate of *altigenis* is decidedly narrow, but that of *ferox* is extreme in this respect. In *ferox* the sagittal crest is high and narrow over the greater part of the brain case; in specimens 1549 and 9999 the sagittal ridge is very low excepting over the most posterior portion of the brain case, where it attains a considerable height. In specimen 9999 the ridge is divided almost to the posterior third of its length by a sharp but very narrow groove. The lambdoidal crest is strong and high.

The broad frontal region is slightly concave in front of the postorbital processes, but is convex immediately behind these points in specimen 1549. The postorbital processes are very short and blunt. The nasal region is characterized by the shortness of the nasal bones, which do not reach back to a line drawn between the anterior borders of the orbits. They are considerably shorter than in *Daphaenus* or in *Mesocyon*.

The zygomatic arch is not especially robust. The postglenoid process is long and acute. The paroccipital process is shorter and less acute than in *ferox*, and is not directed downward as much as in that species.

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[12] J. Eyerman. Amer. Geol., Vol. 17, p. 267.

The anterior and posterior palatine foramina are small. The anterior border of the posterior nares is situated considerably behind the last molars. The nasal chamber is narrow and the inferior borders of the lateral walls are arched inward, giving it a more nearly tubular form than is seen in *Canis*. The lachrymal and optic foramina, and the sphenoidal fissure have much the same relations as in *Canis*. The optic foramen, the sphenoidal fissure, and the foramen rotundum are in a distinct groove separated from the region above by a sharp ridge. The foramen rotundum is very close to the sphenoidal fissure in the recessed posterior end of this depression. The posterior opening of the alisphenoid canal is almost hidden inside the foramen ovale. The postglenoid foramen is nearer the median line of the skull than is the lowest part of the postglenoid process. The relations of the condylar foramen are much as in *Canis*. The foramen lacerum posterius seems relatively small. The postparietal foramina are situated at about half the height of the brain case.

The arrangement of many of the foramina, particularly the postglenoid and the posterior opening of the alisphenoid canal, is much like that in *Daphaenus felina* as described by Hatcher.[13]

Dentition.—The generic characters of the dentition of *Temnocyon* have already been fully discussed by Cope,[14] Schlosser,[15] Scott,[16] Eyerman,[17] Wortman and Matthew.[18] The observations of these writers are only confirmed by the excellent material of *altigenis* now available. These specimens show that in this species the deuterocone of P^4 is extraordinarily large compared with that in most typical canids. The same feature is seen in *ferox*, and the deuterocone of P_4 in *wallovianus* is also larger than is indicated in Cope's figure of this form; so that this character may be considered diagnostic of the genus. The reduced and almost rounded form of

[13] J. B. Hatcher. Oligocene Canidae, Mem. Carnegie Mus., Vol. 1, No. 2, p. 75.

[14] Cope, E. D. Tert. Vert., p. 902.

[15] Schlosser, M. Beitr. z. Pal. Oestr-Ung., B. 4, p. 280.

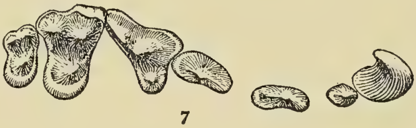
[16] Scott, W. B. Trans. Am. Phil. Soc., Vol. 17, p. 73.

[17] Eyerman, J. Amer. Nat., Vol. 17, p. 268.

[18] Wortman and Matthew. Bull. Am. Mus. Nat. Hist., Vol. 12, p. 115.

the protocone of M^1 is evidently characteristic of *altigenis*, but is not marked in either *ferox* or *wallovianus*. M^2 is relatively larger in *altigenis* than in the other species.

In the inferior dentition P_1, which has not been previously described, is single-rooted and simple crowned. The crown projects over the root anteriorly so that the summit is almost immediately over the anterior border of the alveolus. M_3, which has also been unknown, is a very small tooth somewhat similar in form to M_2. It has very low anterior and posterior tubercles and an antero-internal shelf without tuberculation as in M_2.



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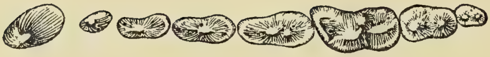

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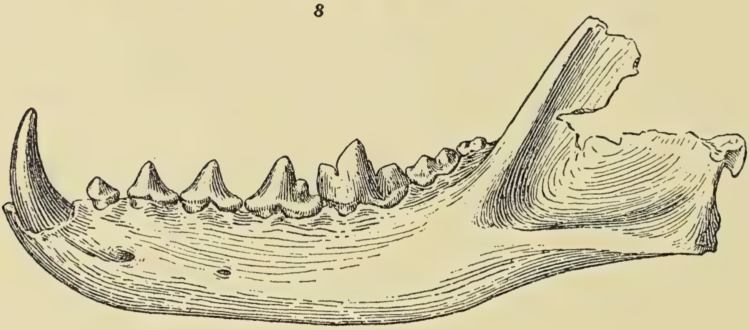

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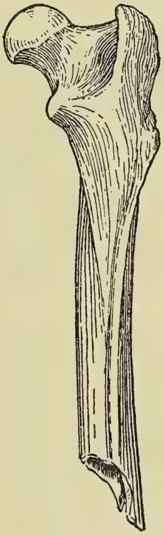
Fig. 7. *Temnocyon altigenis* Cope. Inferior aspect of right superior dental series. No. 9999. John Day beds, Logan Butte, Crook County, Oregon. × $\frac{2}{3}$.

Fig. 8. *Temnocyon altigenis* Cope. Superior aspect of dentition shown in fig. 9. × $\frac{2}{3}$.

Fig. 9. *Temnocyon altigenis* Cope. Outer side of left ramus of the mandible. No. 9999. John Day beds, Logan Butte, Crook County, Oregon. × $\frac{2}{3}$.

Limbs.—Concerning the structure of the limbs, but little can be added to what Eyerman has presented in the description of *ferox*. The limb elements of *altigenis* are perhaps a little more slender than the corresponding elements of *ferox*. In the humerus the shaft is not as straight as in *ferox*. The acute deltoid ridge is extended downward for more than two-thirds the length of the bone. The supinator ridge is prominent, but not as well developed as in *Daphaenus*. The entepicondylar foramen is large. On the femur, the gluteal ridge and spiral line are very strongly marked. The space between them is set off as a perfectly flat, triangular area very distinctly marked off. The extension of the linea aspera below is a long, sharp ridge. The upper portion of the gluteal ridge is considerably enlarged, and is quite distinctly separated from the great trochanter. This tubercular enlargement is really comparable to a reduced third trochanter. As nearly as can be judged from comparison with the figures published by Hatcher,[19] it is similar to the development of the gluteal ridge in *Daphaenus felinus*, though Hatcher stated that a third trochanter was wanting in that form. Eyerman[20] mentions a third trochanter in *Daphaenus*, but I find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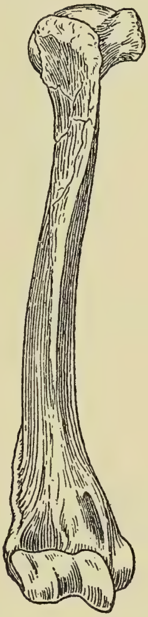
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FIG. 10. *Temnocyon altigenis* Cope. Posterior side of right femur. No. 9999. John Day beds, Logan Butte, Crook County, Oregon. × ½.

FIG. 11. *Temnocyon altigenis* Cope. Anterior side of right humerus. No. 9999. John Day beds, Logan Butte, Crook County, Oregon. ×½.

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[19] J. B. Hatcher. *Op. cit.*, Pl. 19, Fig. 1.

[20] J. Eyerman. *Temnocyon* and *Hypotemnodon*. Amer. Geol., Vol. 17, p. 279, 1896.

no reference in his paper to the character of the femur of *Temnocyon* in this region.

The elements of the epipodial region in both anterior and posterior limbs are stated by Eyerman to be relatively short compared with the propodial segments. Unfortunately no one of these elements is perfectly preserved in specimen 9999, so that the exact measurements of length cannot be obtained. The manus is not preserved. In the pes the principal elements are present excepting the phalanges, and the structure of the foot in the main features resembles that of *ferox*.

Affinities.—In some characters this species seems to be less specialized than *T. ferox*, but in general the stage of evolution is nearly as far advanced. *T. ferox* occurs in the Upper John Day. The best known occurrence of *T. altigenis* is near the boundary between the middle and upper divisions. The relationship of *altigenis* to *wallovianus* is doubtful, though the greater reduction of M^2 in *wallovianus* may indicate that it is a more advanced form. The occurrence of *wallovianus* is unknown.

The relation of the genus *Temnocyon* to the White River *Daphaenus* has been ably discussed by Scott,[21] Eyerman,[22] Wortman and Matthew,[23] Wortman,[24] and more recently by Hatcher.[25] With the support of excellent evidence, the opinion has been generally expressed that *Temnocyon* is in the line of descent from *Daphaenus.* Hatcher has described as the ancestor of *Temnocyon*, a new genus, *Protemnocyon*, based on a new species, *P. inflatus*, from the Oreodon beds. Unfortunately *Protemnocyon* was compared only with Cope's *Temnocyon coryphaeus*, which is quite distinct from the typical *Temnocyon*, and is generally recognized as a separate genus, *Mesocyon.* In some respects, *viz.*, enlarged brain case, lower sagittal crest, and reduced M^3, *Protemnocyon* represents a more advanced type than *Daphaenus*, and in the character of the molars it approaches *Mesocyon* somewhat more closely than does the true *Daphaenus.* The type ancestral to the true *Temnocyon* is approximated more nearly in *Daphaenus vetus*, as previously suggested by several writers.

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[21] W. B. Scott. Trans. Am. Phil. Soc., Vol. 17, p. 73, and Vol. 19, p. 406.

[22] J. Eyerman. *Op. cit.*, p. 283.

[23] Wortman and Matthew. *Op. cit.*, p. 118.

[24] J. L. Wortman. Am. Jour. Sc., June, 1901, Vol. 11, p. 449.

[25] J. B. Hatcher. *Op. cit.*, p. 105.

MEASUREMENTS

	T. ferox type[26]	*T. altigenis* type	No. 9999	No. 1549	*T. wallovianus* type
Length of skull, premaxillaries to inion	266	....	178	....	....
Width of skull between upper borders of orbits	....	....	*a*34	39.5	....
Width of palatine region between canines	18	....	*a*20	20.8	....
Width of palatine region between deuterocones of P^4	....	....	*a*25.4	26.5	....
Width of palatine region between anterior upper molars	24	....	*a*23	25	....
Height of inion above foramen magnum	....	....	32	....	....
Length of superior dentition, posterior side of canines to posterior side M^2	96	70	67	70	67
I^1, transverse diameter	....	....	2	2.4	....
I^3, transverse diameter	....	....	4.4	5	....
Superior canine, antero-posterior diameter at base of enamel	....	....	11	11.9	....
P^1, antero-posterior diameter	11	....	6.5	*a*7	....
P^2, antero-posterior diameter	14	....	10.4	*a*11.4	....
P^2, greatest transverse diameter	....	....	4.5	....	....
P^3, antero-posterior diameter	17	....	12	*a*12.8	13
P^4, antero-posterior diameter	23	19	17	18	17
P^4, transverse diameter across deuterocone	16	12.5	12	13	11
M^1, antero-posterior diameter	16.5	14	13	13.5	12
M^1, transverse diameter	25.3	20	17.75	18.5	15
M^2, antero-posterior diameter	8	7.5	7.3	8	5
M^2, transverse diameter	14	14	12	12	10
Length of mandible, anterior side of canine to condyle	204	....	138	....	....
Height of mandible below P_2	31.6	24	21	....	....
Height of mandible below protoconid of M_1	38.3	28	22	....	....
P_1, antero-posterior diameter	....	....	6	....	....
P_2, antero-posterior diameter	14.8	11	10	....	....
P_3, antero-posterior diameter	14.2	....	11.7	....	....
P_4, antero-posterior diameter	21	15	14.5	....	....
M_1, antero-posterior diameter	21.5	18.5	17.25	....	....
M_1, length of heel	7	7	5.6	....	....
M_2, antero-posterior diameter	13	11.5	10.25	....	....
M_3, antero-posterior diameter	....	....	5.5	....	....
Humerus, length	203.5	....	155	....	....
Calcaneum, length	....	....	50	....	....
Metatarsal 2, length	69	....	56.5	....	....

a Approximate.

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[26] Measurements largely from Eyerman's figures. *Op. cit.*, Pl. 11.

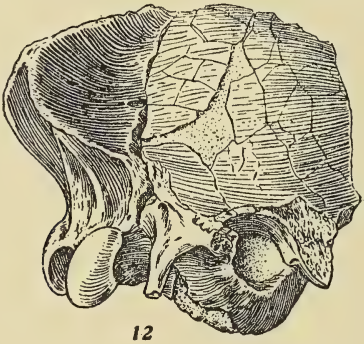
PHILOTROX, New Genus

PHILOTROX CONDONI, new genus and species

Text-figures 12, 13, and 14

Type specimen No. 89, Univ. Calif. Col. Vert. Palae. From the Middle John Day, Turtle Cove, John Day Valley, Oregon.

This form is known from a single specimen found by Mr. L. H. Miller in the Middle John Day beds at locality 819, Turtle Cove, on the John Day River. There is present only the posterior part of the cranium and the left mandible, with nearly complete lower dentition. The teeth are in perfect state of preservation.



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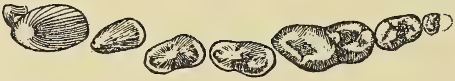

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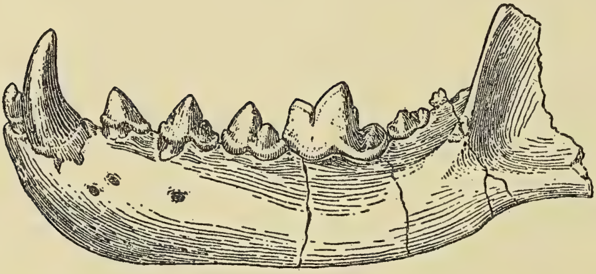

14

FIG. 12. *Philotrox condoni*, n. gen. and sp. Right side of posterior cranial region. No. 89. $\times \frac{3}{4}$.

FIG. 13. *Philotrox condoni.* Superior aspect of mandibular dentition. No. 89. $\times \frac{3}{4}$.

FIG. 14. *Philotrox condoni.* Outer side of mandible. No. 89. $\times \frac{3}{4}$.

Distinctive Characters.—Cranium with well-developed brain case, and large thin-walled auditory bullae. Two pair of postparietal foramina present. Mandible short, uncommonly heavy anteriorly. Dentition $\frac{}{3}$ (?), $\frac{}{1}$, $\frac{}{3}$, $\frac{}{3}$. Premolars heavy, P_2 without basal tubercles, P_3 and P_4 with anterior and posterior basal tubercles and posterior cusp. M_1 with well-developed shear and somewhat reduced metaconid. The somewhat elevated hypoconid occupies about half of the broad heel of M_1, entoconid low. M_2 without prominent paraconid, M_3 in general like M_2.

Skull.—The fragment of the cranium shows a brain case and posterior cranial crests of moderate proportions. The crests are about as prominent as in *Mesocyon coryphaeus*. The otic bulla present is thin-walled and large. It is almost entirely separated from the postglenoid process. The paroccipital process is slender. There are two postparietal foramina, of which the larger, anterior one is situated a little more than half way up the side of the brain case and in front of the lambdoidal crest. The smaller, posterior foramen is located considerably higher up and on the base of the lambdoidal crest, much as in the postparietal foramina of *Enhydrocyon*. The postglenoid foramen is situated very close to the median border of the postglenoid process. The situation of the condylar foramen is much as in *Canis*.

The mandible is short and the posterior end of the dental series is considerably elevated. The anterior portion of the jaw is more than ordinarily heavy. The inferior border is only slightly convex. The massateric fossa reaches forward to a point below the posterior end of M_2.

Dentition.—The dentition, so far as known, is $\frac{}{3}$ (?), $\frac{}{1}$, $\frac{}{3}$, $\frac{}{3}$. Viewed from above, the dental series is seen to curve toward the median line rather sharply in front of the last premolar as in other short-jawed forms. The enamel of all the teeth is more or less rugose.

Only one incisor, I_3 (?), is present in the jaw. It is a relatively small tooth with a small lateral cusp which is only a little lower than the principal cusp. The symphyseal region is uncommonly narrow and the space between the outer incisor and the symphysis is occupied by an antero-posteriorly elongated pit which does not include more than half of the area. A very small incisor evidently representing I_2 or I_1 was found loose in the matrix with the mandible. It would occupy only about half of the empty alveolus, but if the other incisor was present, one of them must have been crowded far back.

The canine is large and is somewhat heavier than in most of the associated canid forms.

Of P_1 there is no trace, though the alveolar border is perfectly preserved, and as P_2 is large and very near the canine, its absence is evidently normal. All three of the premolars are rather heavy. The first two are set somewhat obliquely in the jaw. All three are two-rooted. P_2 has no distinct anterior or posterior tubercles, though the cingulum is slightly swollen anteriorly and posteriorly. P_3 has a minute anterior basal tubercle, a posterior cusp, and an incipient posterior basal tubercle. The general structure of P_4 is similar to that of P_3, but the basal tubercles and posterior cusp are better developed.

The shear of the trigonid on M_1 is thick at the base and the blades are relatively higher than in *Canis*. The metaconid is about as large as in *Canis*. On the talonid, the base of the hypoconid does not reach inward beyond the middle of the heel. The summit of this cusp is laterally compressed, but is not as high as in *Temnocyon*. The inner half of the talonid is slightly excavated, and there are two small tubercles corresponding to the entoconid and hypoconulid on its inner and posterior borders.

M_2 shows a well-developed protoconid and metaconid, the former being somewhat the larger. On an excavated antero-internal shelf a low marginal ridge represents the paraconid. The heel is slightly hollowed and the outer border is a little higher than the inner.

The structure of the small M_3 is so far as known in general similar to that of M_2, though the paraconid shelf is smaller.

Affinities.—The type of canid described above shows considerable resemblance to the short-faced dogs which have been grouped together in the sub-family Simocyoninae. Of these there are known from the John Day three genera, *Oligobunis*, *Hyaenocyon*, and *Enhydrocyon*, no one of which corresponds closely to the form under discussion.

Oligobunis differs in having four inferior premolars and two molars instead of three premolars and three molars; in the absence of an anterior basal tubercle on P_3; in the shorter heel of M_1; and in the greater width of M_2. The metaconid of M_1 in *Oligobunis* appears from Cope's figures to be considerably larger than in *Philotrox*, and the anterior portion of the lower jaw is more slender.

The imperfectly known *Hyaenocyon* has apparently the same number of inferior premolars as *Philotrox*, but in *H. basilatus* they are somewhat heavier and the anterior basal tubercles are much better developed. P_2 is markedly trilobate in this species, but is without accessory tubercles in *Philotrox*. This tooth is also relatively much smaller in *Hyaenocyon*. There is little correspondence between the inferior dentition of *Philotrox* and the dentition of *H. sectorius* in form and arrangement of the teeth. The sectorial portion of the inferior carnassial of *Philotrox* is exceedingly narrow antero-posteriorly compared with the fore and aft diameter of the upper carnassial in *H. sectorius*. The presence of the third lower molar in *Philotrox* indicates the existence of at least two molars in the upper series, while Cope confidently states that there was but a single superior molar in *H. sectorius*.

The lower jaw of *Enhydrocyon* is unfortunately even more imperfectly known than that of *Hyaenocyon*. There are probably three inferior premolars in this genus, though P_2 is unknown. The premolars are at least specifically distinguishable from those of *Philotrox*, and P_3 has no anterior basal tubercle. The heel of M_1 in *Enhydrocyon* appears to be narrower posteriorly than in *Philotrox*, and has, according to Cope,[27] "an absolutely median cutting edge." There is, however, a rudimentary entoconid at the base of this cusp. The first tubercular is apparently also rather of the lacinate type, possessing "a nearly median cusp in front, which is joined to the low one on the internal border of the crown." It is not known whether M_3 was present. In the skull of *Enhydrocyon* the single pair of postparietal foramina are larger but are apparently situated much as the posterior pair in *Philotrox*. The otic bullae in both genera are extraordinarily large.

Tomarctus Cope from the Loup Fork Miocene of Colorado is evidently a more specialized form, both as regards the reduction of the premolars and the development of M_1.

Philotrox resembles the Old World Simocyonines in the shortness of the jaw, and the rather heavy type of the premolars. It differs from *Simocyon* in the greater development of P_2 and P_3, in the much smaller size of M_2, and in the presence of M_3. The heel of M_1 is also less distinctly basin-shaped in *Philotrox*. From *Cephalogale* it is distinguished by the absence of P_1 and the greater development of P_2 and P_3. The cusps of the lower carnassial are also somewhat more elevated and the metaconid seems to be less prominent. In other respects there is much in common with *Cephalogale*, particularly in M_2 and M_3, and in the form of the heel of M_1.

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[27] E. D. Cope. Tertiary Vertebrata, p. 938. Also, *ibid.*, "The heel of the sectorial is cutting, as in *Temnocyon*." . . .

Of the five genera referred to the Simocyoninae all are removed from *Philotrox* by quite a distance. *Cephalogale* is possibly one of the nearest, while *Simocyon* is one of the farthest removed. *Oligobunis* is evidently not closely related; *Enhydrocyon* and *Hyaenocyon* appear to be about as far removed as *Oligobunis*, but are not well enough known to warrant a definite statement.

In the present state of our knowledge it is difficult to determine exactly the relative stages of evolution reached by the John Day types of short-faced dogs. *Philotrox* does not appear to represent either the most primitive or the most specialized type of the four genera. As far as is known, it seems to show a somewhat higher development of the crushing functions in the tubercular region of the inferior molars than we find in the other forms.

It is also difficult to make even a tentative statement as to the probable origin of *Philotrox*. While it exhibits some resemblance to *Cephalogale*, it is to be doubted whether its affinity in this direction is really closer than with some of the members of the *Cynodictis* group. Particularly is this true of the cusps of the inferior sectorial which are hardly of the type of *Cephalogale*. I am inclined to accept the suggestion of Wortman[28] that a member of the White River genus *Daphaenus*, like *D. dodgei*, may lead to some of the short-jawed dogs of the John Day. The evidence of relationship to this form seems at least as strong in the case of *Philotrox* as in any of the other genera. *D. dodgei* has a rather short, heavy jaw. Excepting P_1, which is much reduced, the premolars are heavy, and possess posterior cusps. The heel of M_1 is broad and basin-shaped, the form and arrangement of its three tubercles appearing to be much the same as in *Philotrox*.

So great is the diversity of form among the four genera of short-faced John Day dogs that it is difficult to determine from the material available whether we are warranted in considering them all as descendants of the same stock. If such similarities as they show are actually an expression of common ancestry, it would seem that we find at least as many of the necessary characters of this ancestral type in the North American *Daphaenus*, as in *Cephalogale* or in any of the European genera.

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[28] J. L. Wortman. Am. Jour. Science, June, 1901, Vol. 11, p. 449.

The relationships of the previously known short-faced John Day dogs to the European Simocyonines seem in a general way to be far from close. The affinity with *Cephalogale* is presumably not as close as with *Daphaenus*. Compared with *Simocyon*, we find the dentition differing in each genus about as widely as it could be made to differ and still keep them short-faced, heavy-toothed canids. No single functional cheek tooth of *Simocyon* shows much resemblance to the corresponding tooth of *Oligobunis*. This would be true also of the inferior cheek teeth and upper carnassial of *Enhydrocyon*. The upper molars of *Enhydrocyon* are too imperfectly known for comparison. In *Hyaenocyon* the inferior cheek teeth are different, as far as known. The superior sectorial suggests a structure somewhat similar to that of *Simocyon*, but M_1 is much smaller and there was no second superior tubercular.

It is to be expected that differentiation will tend to produce short-faced, heavy-toothed carnivores of the hyaenoid type as often and in as many places as circumstances will permit. The Hyaenidae represent an Old World adaptation in this direction. They have come to differ so far from the other groups of the Carnivora Vera and to fill such an important place in eastern Arctogaea that they are separated as a distinct family. Whatever the ancestors of the hyaenas may have been, they were probably not true canids. A somewhat similar adaptation has occurred in the Canidae. So similar have the results been in the two cases, as far as function and superficial characters are concerned, that several canids from the American faunas have found temporary location with the hyaena group in the classification.

It appears more than probable that the development of hyaenoid characters in the Canidae has gone forward to a great extent independently in North America and Europe, and has, moreover, produced quite different results in the two regions. It is not improbable that there has been mixing of the resultant types through migrations, though we have as yet little evidence of such intermigration. Unless we can discover more definite evidence of common descent of the American and European genera than has yet been brought forward, it must appear that the sub-family Simocyoninae as generally accepted, including *Simocyon*, *Cephalogale*, *Oligobunis*, *Enhydrocyon*, and *Hyaenocyon*, is a group of polyphyletic origin, representing a general type of adaptation rather than similar characters expressive of common origin. At the present time we are not even in a position to state definitely that all of the genera mentioned are really typical canids. The continuance of their definite arrangement in one sub-family will serve only to cover up certain weak places in our phylogenies, and ultimately to impede the progress of knowledge.

MEASUREMENTS

	mm.
Length, anterior side of inferior canine to posterior side of M_1	63
Length, posterior side of inferior canine to posterior side of P_4	35.5
Height of mandible below middle of P_2	21.5
Height of mandible below protoconid of M_1	19.5
I_2 (?), transverse diameter	2.8
I_3, transverse diameter	4
Inferior canine, length from unworn tip to alveolar border	21.5
Inferior canine, greatest antero-posterior diameter at base	10.5
P_2, antero-posterior diameter	8.3
P_2, transverse diameter	5.2
P_3, antero-posterior diameter	10.5
P_4, antero-posterior diameter	11.6
P_4, transverse diameter	6.5
M_1, antero-posterior diameter	18.0
M_1, transverse diameter of trigonid	7.8
M_1, antero-posterior diameter of heel	5
M_1, transverse diameter of heel	7.1
M_2, antero-posterior diameter	8
M_2, transverse diameter	5.4
M_3, antero-posterior diameter	*a* 5
Height of inion above foramen magnum	33
Greatest width across occipital condyles	34.5
Height of foramen magnum	12
Greatest antero-posterior diameter of otic bulla	28.5
Greatest transverse diameter of otic bulla	19

a. Approximate.

FELIDAE

Though fairly well known from skulls and teeth, the John Day cats have, as a whole, presented some of the most puzzling features of this fauna. The most common and best known forms included in the genera *Archaelurus* and *Nimravus* have been generally considered as representing the most primitive division of the machaerodont group of the Felidae. In the White River beds, held to be older than the John Day, there appeared to be among the felines no forms so primitive as these. As the other elements of the John Day fauna are nearly all more advanced than the corresponding forms of the White River, the evidence regarding the age of the beds which is furnished by these cats seemed to contradict that of the remainder of the fauna.

Much yet remains to be learned concerning the John Day cats, as in most cases but little excepting the skull and dentition has been discovered.

No representatives of the Felidae have been described from the Mascall beds.

The following species are known from the John Day series:—

Archaelurus debilis Cope.
Nimravus gomphodus Cope.
Nimravus confertus Cope.
Deinictis cyclops Cope.
Pogonodon platycopis Cope.
Pogonodon brachyops Cope.
Pogonodon davisi, n. sp.
Hoplophoneus cerebralis Cope.
Hoplophoneus strigidens Cope (?).

NIMRAVUS and ARCHAELURUS

Pl. 4; Pl. 5, Figs. 1 and 2; and Text-figures 15 and 16

Generic and Specific Distinctions.—The genera *Archaelurus*[29] and *Nimravus*[30] were established by Cope to include three feline species related to the sabre-tooth forms but having very primitive characters. They were referred to by Cope as the "false sabre-tooths," owing to their lack of a prominent flange on the antero-inferior angle of the lower jaw, and the absence of a cutting edge on the anterior side of the relatively short upper canines. There was also noticed in both genera a peculiar exostosis or a thickening of the outer side of the alveolar border immediately below the inferior molars. Neither genus was known outside the limits of the John Day series. Of the two, *Archaelurus* was said to be the more primitive, having one more premolar in each jaw, and smooth-edged instead of posteriorly serrated upper and lower canines. Other differences between the single species of *Archaelurus* and the two placed in *Nimravus* were supposedly of no more than specific value.

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[29] *Archaelurus.* Am. Nat., Vol. 13, Dec. 4, 1879, p. 798*a*–798*b*.

[30] *Nimravus.* Proc. Acad. Nat. Sc., Philad., Aug. 12, 1879, pp. 169 and 174.

Though *Archaelurus* and *Nimravus* appeared to Cope to be quite distinctly separated, studies of recently discovered material show that they are scarcely separable if not identical generic types. In the University of California collections there are several specimens which show the skull and dentition of forms belonging in this group more perfectly in some particulars than they were exhibited in the types.[31] All of this material indicates that *Archaelurus* is not so distinctly separated from *Nimravus* as it was considered to be by Cope.

In a particularly well-preserved skull (No. 1681), pl. 4, and text-figure 15, there is a mixture of the characters of *Archaelurus* and *Nimravus*. As in *Archaelurus debilis*, there are four superior premolars. The upper canine is slightly shorter and appears to show a little more curvature than in *Nimravus*, but in other characters it differs greatly from *Archaelurus* as described, and in these particulars resembles *Nimravus*. The posterior side instead of being smooth-edged is strongly compressed and has a sharply serrated margin. As in *Nimravus*, the anterior side is broad, and is slightly concave toward the inner angle. The outer anterior portion is rounded. The inner anterior angle is acute, and is noticeably serrated toward the base of the tooth. In this last character it is even more specialized than the corresponding portion of this tooth as described for *N. gomphodus*. The skull in which this dentition occurs represents an individual much larger than the type of *A. debilis*. In dimensions it is nearest to the type of *N. gomphodus*, the largest described form referred to either of these genera, but it exceeds this specimen in axial length by about 20 millimeters.[32]

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[31] This material includes the following specimens: No. 1681, perfect cranium without mandible, with axis and one other cervical vertebra; No. 1685, cranium with dentition, lacking I^1 and the frontal region; No. 1679, mandible with dentition; No. 1680, middle portion of mandible with P_3 and M_1, also five lumbar vertebrae; No. 1683, half of mandible with M_2 and parts of other teeth; No. 2256, nearly complete hind limb; No. 110, perfect tibia, calcaneum, fragments of metapodials, caudal vertebrae. In addition to these there are a number of loose teeth and scattered limb bones.

It is difficult to determine the affinities of this form, judging solely from the characteristics which appeared in the type specimens. As the form represented by specimen No. 1681 is separated from *Archaelurus* principally by the character of the margins of the superior canine, the writer has examined the type specimen of *Archaelurus* with a view to verifying Cope's statement regarding this tooth. It was found, however, that the posterior margins are really serrated instead of smooth, Cope having been deceived apparently by the worn surfaces of the tooth. The anterior sides were so much worn that it was not possible to determine their exact form. The evidence available seems to me to indicate that no sufficient generic distinctions are to be obtained in the character of the canines. Though slight differences in the structure of the margins may exist, it is very doubtful whether such variations in general form as may be present are of more than specific value.

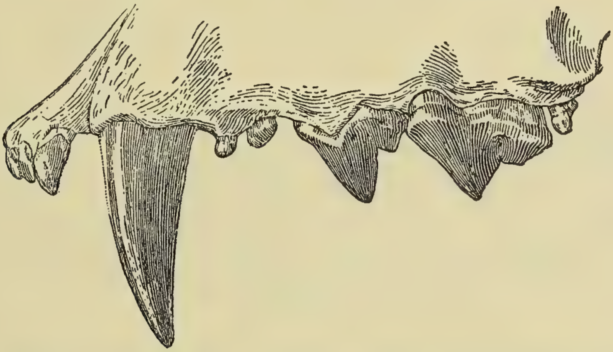

FIG. 15. *Archaelurus debilis major.* No. 1681. Middle John Day, Logan Butte, Crook County, Oregon. × $\frac{3}{4}$.

As to the other generic character used by Cope, namely, that based upon the number of premolars, Cope's type of *N. gomphodus* shows no indication of the presence of premolar one in either the upper or the lower jaw, but as this tooth is exceedingly small in *Archaelurus* it is easily conceivable that it would disappear in many cases. In the collection of Professor Thomas Condon, at the University of Oregon, there is a well-preserved feline skull which was studied by Cope and was labeled *N. gomphodus* by him. In this individual there are but two inferior premolars. In the specimen as it was studied by Cope there appeared to be only three upper premolars, but more careful preparation of the upper jaw has shown an alveolus for a fourth, or P^1. In whichever genus this species is placed the dentition of one jaw will represent the other genus.[33]

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[32] Axial length of skull. Type *A. debilis*, 180 mm. Type *N. gomphodus*, 206 mm.; No. 1681, 225 mm.

The differences between the types of *Archaelurus* and *Nimravus*, or *A. debilis* and *N. gomphodus*, are perhaps most strongly expressed in the lower jaws. In Cope's material, *A. debilis* was characterized by the presence of a very large exostosis below the molars, while in *N. gomphodus* this was represented by only a slight swelling of the external alveolar border. According to Cope, this thickening was "larger in some specimens than in others." *N. gomphodus* was supposed to be further characterized by the absence of P_2, absence of an anterior basal tubercle on P_3, and the failure of the massateric fossa to reach the inferior border of the ramus at any point.

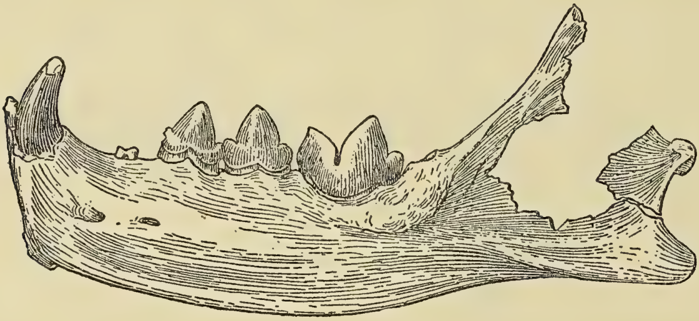

FIG. 16. *Archaelurus debilis major.* No. 1679. Middle John Day, Blue Basin, Turtle Cove, John Day Valley, Oregon. × ½.

As in the crania described above, the mandibles in the University collections all show more or less mixing of characters. A large specimen (No. 1679, text-figure 16) exceeds the type of *A. debilis* in size by about 30 per cent. Its dimensions are in general near those of the type of *N. gomphodus*, but it is even larger than that form, and apparently represents the largest known individual of this group. The exostosis is intermediate in size between the slight thickening in *N. gomphodus* and the greatly inflated alveolar border of *A. debilis.* The massateric region is similar to that of *Archaelurus*, but the mandible is relatively higher below the diastema than in the type specimen. The posterior angle of the canine is denticulate, as in *Nimravus.* P_2 is double-rooted instead of single-rooted as described for *Archaelurus* by Cope, but a re-examination of the type shows that it is two-rooted there also. P_3 possesses a small anterior basal tubercle as in *Archaelurus.*

---

[33] Judging from Condon's figures (The Two Islands, Pl. 20, opposite p. 124), the superior canine and mandible are of the *Archaelurus* type.

In another specimen (No. 1680), representing the median portion of the jaw, the inferior canine, and several lumbar vertebrae, the dimensions are intermediate between those of *A. debilis* and the large specimen described above. The exostosis is little if any larger than in *Nimravus*, and the canine shows posterior serration, but the massateric region is apparently as in *Archaelurus.* The height of the jaw seems to be relatively less than in the larger specimen. As in *Archaelurus*, P_2 is double-rooted and P_3 has a weak anterior basal tubercle.

A third and much smaller mandible (No. 1683) shows the weak exostosis of *N. gomphodus* and the double-rooted P_2 of *Archaelurus.* The inferior portion of the jaw is broken away, but the massateric fossa extends far forward as in *A. debilis.* In this specimen the diastema, to P_2, is very short and the median portion of the inferior side of the symphyseal region is rather prominent. The well-preserved M_2 is laterally compressed and has a divided root. It shows a sub-acute superior ridge which is divided into a median tubercle and distinct anterior and posterior basal ridges.

The relative dimensions of these individuals compared with those of the described species of *Archaelurus* and *Nimravus* are brought out in the following table:—

	N. gomphodus type	No. 1679	No. 1680	*A. debilis* type	No. 1683	*N. confertus* type
Length of mandible, anterior side of symphysis to posterior side of condyle	158	*a*175	....	140	....	....
Height of mandible below middle of diastema	27	31	....	20	20	20
Height of mandible at posterior end of P_4	31.5	37	....	24	....	....
Length, posterior side of canine to anterior side of P_2	....	16	....	14.5	10	....

	N. gomphodus type	No. $\overline{1679}$	No. $\overline{1680}$	*A. debilis* type	No. $\overline{1683}$	*N. confertus* type
Length, posterior side of canine to anterior side of P_3	23	25	....	21	18.5	12.5
Antero-posterior diameter of P_3	17	17	15	14	....	13.3
Antero-posterior diameter of P_4	20	19.5	....	15	....	16
Antero-posterior diameter of M_1	25	27	26	....	....	22.5

a Approximate.

The mandibles described above correspond generically to *Archaelurus* and differ from the two species of *Nimravus* in the presence of P_2 and in the characters of the massateric fossa. In the two specimens in which P_3 is present it supports an anterior basal tubercle as in *Archaelurus*. In each individual, however, some considerable deviation from the type of *Archaelurus* is seen, and in all cases this variation is toward the type of *Nimravus*.

Specifically the individuals described above are not readily fitted into any of the known groups. The largest specimen, No. 1679, exceeding both *A. debilis* and *N. gomphodus* in size, belonged to an individual slightly larger than that represented by the skull No. 1681 described above (p. 514). These two specimens probably represent the same species, which is possibly a variety of *A. debilis*, or as suggested by the size and by the reduction of the exostosis, it is perhaps a variant from the *N. gomphodus* type. Until more is known of the variation in the group this form may be tentatively known as *Archaelurus debilis major*.

The slightly smaller mandible, No. 1680, corresponds closely to *N. gomphodus* in size, and possesses only a rudimentary exostosis. As P_2 was present and P_3 has an anterior basal tubercle, this specimen may be tentatively referred to *A. debilis major*.

The third specimen, No. 1683, has nearly the same dimensions as the type of *A. debilis*, and is referred to that species, though as in *N. gomphodus* the inferior portion of the symphyseal region is prominent and the exostosis much reduced.

The great variation in size and form of the exostosis among these and other known specimens indicates that, as suspected by Cope, this structure cannot be used in generic separation and only doubtfully in distinction of the species. The value of the anterior basal tubercle on P_3 in separating the genera must also be doubtful, as the difference between the small anterior tubercle in *Archaelurus* and the rather prominent anterior basal angle in *Nimravus* is slight. The presence of P_2 in *A. debilis* is of doubtful value as a distinguishing character. It is a very small and practically functionless tooth, and its occurrence would naturally be variable. While it is usually present in specimens with the *A. debilis* type of massateric fossa and showing an anterior basal tubercle on P_3, it is also associated with a posteriorly serrated inferior canine and a greatly reduced exostosis. It is absent from Professor Condon's specimen in which the superior premolar dentition is that of *Archaelurus*. Practically the only character which seems distinctive is found in the form and size of the massateric fossa. In *N. gomphodus* its inferior margin is separated from the lower border of the horizontal ramus by a wide bar. In *A. debilis* the fossa extends farther forward and reaches down to the inferior margin of the jaw, which it may follow for some distance.

In the present state of our knowledge there appear to be three or four types represented in the *Archaelurus-Nimravus* group. It is not certain that they represent distinct species and the number will possibly be reduced when more material is known.

A. debilis is a small form representing the more primitive extreme in premolar dentition and possibly in the form of the canines. P_3 has an anterior tubercle. The massateric fossa is relatively broad and the exostosis is large. The type skull is 180 mm. long, P^1 and P_2 are both present, the canine is not greatly elongated. It represents a fully adult individual and possibly a female.

A. debilis major. Large forms with variable premolar formula, reduced exostosis, and wide massateric fossa. Superior canines moderately elongated, with serrated posterior edge, and with basal anterior groove. Type skull No. 1681 (pl. 4), a young individual; basal length 225 mm. Mandible No. 1679 (text-figure 16), referred to this species, is from a somewhat larger individual with teeth but little worn. The inferior canine has a serrated posterior margin, P_2 is two-rooted, P_3 with anterior basal tubercle, and the exostosis is somewhat reduced. These two young specimens exceed the old individual representing the type of *debilis* by more than 45 mm. in skull length, which is more than the ordinary range of sexual variation in cat skulls of approximately this size.

N. gomphodus has a generally reduced premolar dentition, lacking both P^1 and P_2. The canines are relatively long and slender, though both characters are doubtless somewhat exaggerated in the type specimen. P_3 without distinct anterior basal tubercle. Massateric fossa relatively narrow. The skull characters separating this species from *A. debilis* are largely bridged over by *A. debilis major.*

N. confertus resembled *N. gomphodus* excepting in the character of the greatly shortened inferior diastema. Known only from the lower jaw.

The observations presented above indicate some of the difficulties met in attempting to carry a separation of the generic groups *Archaelurus* and *Nimravus* beyond the type material. It should be stated further that a somewhat similar mingling of characters of these genera is encountered in a study of the structure of the skull, limbs, and vertebrae. As far as is known, nearly all the supposed diagnostic characters seem to be variable and untrustworthy, excepting possibly the form of the massateric fossa, and it is doubtful whether more than specific value attaches to this feature. The group as a whole seems to show much individual variation, and under these circumstances a thoroughly satisfactory arrangement of the species and genera can be accomplished only by the study of much larger collections than are now available. Cope's collection seems to have contained in the types of *A. debilis* and *N. gomphodus* two rather extreme variants. Neither of these extremes has been met outside of the type collection. Although the larger part of the known material is not included in Cope's collections, all of the specimens range between the limits of these two forms.

Collectively the forms in the *Nimravus-Archaelurus* group represent a fairly distinct feline type. They are characterized in skull and dentition by the absence of a prominent flange on the antero-inferior angle of the mandible; a tendency toward full representation of the premolars; absence of deuterocone on P^4, of protocone on M^1, and of metaconid on M_1; incomplete development of the anterior cutting edge on the superior canines; the presence of a small M_2 and of a peculiar exostosis on the external alveolar margin adjacent to it; and the slight inferior projection of the posttympanic process and of the root of the zygomatic process of the squamosal. This group corresponds in rank to the average genus and, unless further additions to the available material should bring out more definite distinguishing characters, the later name, *Archaelurus*, will probably be ultimately eliminated.

As has been recognized particularly by Adams,[34] the members of the *Nimravus-Archaelurus* group show strong resemblances in dental and cranial characters to *Ailurictis* of the European Oligocene and, as indicated below (p. 525) under the discussion of the extremities, this similarity extends also to the limb structure. There are still a number of characters separating them which may as a whole distinguish the groups sufficiently to permit our continuing them as distinct genera. *Ailurictis* appears, however, to be closely related to the American genera and to represent the same division of the Felidae.

MEASUREMENTS

Skull of *Archaelurus debilis major*, No. 1681

	mm.
Axial length from anterior side of premaxillae to posterior side of occipital condyles	225
Axial length from anterior side of premaxillae to anterior side of inferior narial openings	87
Greatest width across zygomatic arches	150
Width of palate between inner roots of P^4	56
Height of inion above foramen magnum	39
Height of antero-inferior side of orbit above alveolar border at P^4	36
Length, anterior side of superior canine to posterior side of M^1	81.5
Length, anterior side of P^3 to posterior side of M^1	48
Superior canine, length, tip to alveolar border on incompletely erupted tooth	38
Superior canine, antero-posterior diameter at base	16.5
Superior canine, transverse diameter at base	9.2
P^1, antero-posterior diameter	3.9
P^2, antero-posterior diameter	6.6
P^3, antero-posterior diameter	20.5
P^4, antero-posterior diameter	24
P^4, transverse diameter across inner root	15
M^1, antero-posterior diameter	5.7
M^1, transverse diameter	8

Limbs.—Several specimens in the University collection show considerable parts of the appendicular skeleton of feline forms which are very near *Archaelurus*. Among these there is a hind limb, No. 2256 (pl. 5, fig. 1), lacking only the terminal phalanges.

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[34] G. I. Adams. Extinct Felidae, Am. Jour. Sc., 1897, Vol. 154, p. 146.

This furnishes for the first time sufficient material for satisfactorily determining the foot structure in this group. The specimen evidently represents a form close to *A. debilis*, though somewhat larger. It is here tentatively referred to *A. debilis major*.

The femur is much like that of *Nimravus gomphodus* as described by Cope.[35] It differs from this type in that there is no groove connecting the shallow pit for the round ligament with the neck. Unfortunately the femur of *Archaelurus debilis* was not known to Cope.

The tibia is similar to that described for *A. debilis*, excepting for its larger size, and that there are two grooves for the tendons passing over the posterior side of the internal malleolus on this specimen as in existing felines. This is also the case in another and more nearly perfect tibia (No. 110, pl. 5, fig. 2) showing also the characters of *Archaelurus*. In the type of *A. debilis* there is stated to be but one groove.

The astragalus duplicates the peculiar structure seen in *A. debilis*, having a very short neck and a rather long inner border of the trochlea. The internal trochlear ridge is separated a little farther from the distal end of the neck than in *A. debilis*, but a series of otherwise similar specimens of this type shows a slight variation in this character. As has been suggested by Scott,[36] a small facet on the external side of the distal end of the neck corresponds in position to the cuboid facet of the Ursidae. This facet is, however, continuous with the surface of articulation for the sustentaculum and its articulation probably did not reach beyond the calcaneum. The cuboid articulates closely with a distinct facet near the distal end of the external face of the ectocuneiform, and is not higher than the ectocuneiform and navicular as it is in the bears. It shows, moreover, no facet for articulation with the astragalus.

The calcaneum exhibits a strongly marked fossa external to the outer astragalar facet somewhat similar to that seen in *Pogonodon brachyops*, though not so deep as in that form. The sustentacular facet is very long, reaching forward to the extreme anterior end of the bone. Separated from the anterior end of this facet by a sharp angle is a small face in articulation with the navicular. In specimen No. 110 the fossa external to the outer astragalar facet is deeper and the sustentacular facet shows a slight median interruption.

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[35] Tert. Vert., p. 970, Pl. 74, Fig. 2.

[36] W. B. Scott. Osteology of Dinictis felina, Proc. Philad. Acad., July 30, 1889, p. 226.

The navicular is considerably produced posteriorly, as was suggested by Cope from his study of the navicular facet of the astragalus. In this specimen the outer side bears a distinctive mark in the presence of a deep pit opposite the middle of the astragalar facet. The cuboid is a little higher than wide and shows a deep peroneal groove. The mesocuneiform and entocuneiform are small and narrow.

The form of the metatarsals shows the foot to be more specialized than might have been inferred from a study of the skull and dentition. Compared with the size of the tarsus, the middle metatarsal is long and relatively heavy. The total length of the tarsus, measured to the posterior end of the calcaneum, is a little less than that of metatarsal three. In most felines, particularly in the older forms, the tarsus is considerably longer than the metatarsus. This is particularly noticeable in *Hoplophoneus* and to a less extent in *Deinictis*.

The lateral digits are relatively reduced. Metatarsal three is considerably larger and heavier than the others, while number five is relatively short and slender. Number two is also considerably reduced. The proximal end of number two has been somewhat damaged, so that it is not possible to determine certainly whether the foot retained a part of metatarsal one. A small depression on the median or free side of the proximal end of this element, but scarcely reaching beyond the proximal end of metatarsal three, may have been occupied by a rudimentary metatarsal one. As the distal end of the entocuneiform is very thin and slender, such a rudiment if present at all must have been very small.

The reduction of the lateral digits is greater than that in *Deinictis* and *Hoplophoneus*, or than in many of the typical modern cats. A somewhat similar relative elongation of the middle metatarsals and reduction of the lateral ones is seen in the cheetah and caracal.

A slenderness of the anterior foot is indicated by Cope's statement[37] that the fifth metacarpal was relatively much smaller than in the typical modern Felidae.

The terminal phalanges are not known in association with other determinable skeletal elements. The other phalanges are rather broad. The middle phalanx in each digit shows considerably less oblique excavation of the shaft on the outer side than is seen in the modern Felidae with strongly developed retractile terminal phalanges.

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[37] Tert. Vert., p. 961.

Of the relative length of the whole limb no very definite estimate can be made, as complete limb segments have not been found associated with the skull or vertebrae. Comparative measurements of the specimen in which the pes is present with broken tibia and femur (No. 2256), and of No. 110, with complete tibia and calcaneum, indicate that the tibia was a little shorter than the complete pes. An approximation of the proportions in *Archaelurus* compared with those of *Deinictis* seems to show that the tibia has about the same relative proportion to the skull length in the two forms. Compared to the length of the tibia, the combined lengths of the tarsus and metatarsus appear to be a little greater in *Archaelurus*. The relatively long middle metapodials, the reduced lateral metapodials, and the relatively long tibia point toward a type of limb like that seen in the cheetah or hunting leopard rather than toward the type of the lion or tiger. It is also interesting to note that in the loss of the deuterocone of P^4, and in the relative strength of the middle premolars the dentition shows the same resemblances.

In his admirable discussion of the White River sabre-tooths, Dr. W. D. Matthew[38] has suggested that we may "... explain the apparent conservatism in the *Deinictis* dentition by the assumption that its prey consisted in greater part of the smaller, speedier animals of the plains, which it must run down by superior speed or endurance, while the *Hoplophoneus* preyed more on the larger, slower animals of the plains or forest, whose destruction required a more powerful animal with more effective weapons of attack." This suggestion will, I believe, account for the persistence in the John Day of a type like *Archaelurus* with certain apparently primitive characters in its dentition. The greater the specialization of the feet for running, the less useful would they be for grasping, and the less would be the value of greatly elongated superior canines. The presence of long, knife-like canines is correlated with powerful grasping feet possessing highly developed retractile claws. With its powerful feet the animal clung to its prey while it struck repeatedly with its thin, sharp sabres. When the canines are not developed to the dagger-like form for stabbing, the premolar teeth serve a more definite purpose in the destruction of prey, and would be less subject to reduction.

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[38] Mem. Amer. Mus. Nat. Hist., Vol. I, Part 7, p. 394.

The view suggested above finds support, in that such evidence as we have indicates that during the deposition of the Middle John Day beds this region was in the main a country of open plains, offering advantages to running types of carnivores, and that during this epoch the *Archaelurus-Nimravus* type of feline was by far the most common form.

As might be surmised from the known similarities in cranial and dental characters, the foot structure of *Archaelurus* shows considerable resemblance to that in the genus *Ailurictis* of the European Oligocene. As has been shown by Schlosser,[39] metatarsal one is greatly reduced in *Ailurictis*, and particularly the middle metapodials are rather heavy. These characters, as also the unusual elongation of the proximal, external tubercle on metatarsal five, are distinctive features of *Archaelurus*. The limb structure differs somewhat in the two groups in that metatarsals two and five are somewhat less reduced in *Ailurictis*, and the astragalus is stated to show close resemblance to that of *Felis*, while in *Archaelurus* this element has a different and quite distinctive form. As far as can be determined, *Archaelurus* seems slightly more advanced than *Ailurictis* in foot structure.

MEASUREMENTS

A. debilis major, No. 2256

	mm.
Femur,[40] antero-posterior diameter of head	22.8
Femur, transverse diameter of shaft near middle	22
Femur, transverse diameter of distal end	50.5
Femur, width of rotular face at middle	18
Tibia, transverse diameter at distal end	33.5
Tibia, transverse diameter at proximal end	48
Tibia, antero-posterior diameter at proximal end	52
Calcaneum, greatest antero-posterior diameter	67
Astragalus, greatest antero-posterior diameter	36
Astragalus, antero-posterior diameter through trochlear region	28.3

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[39] M. Schlosser. Beiträge zur Palaeont. Oestr-Ung., B. 6, p. 431.

[40] The shaft of the bone has been shattered in the femur and tibia so that the length could not be accurately determined in this specimen.

	mm.
Astragalus, greatest width of trochlear surface	20
Cuboid, greatest antero-posterior diameter on superior surface	17
Combined antero-posterior diameter of calcaneum and cuboid in position	82
Width of tarsus, cuboid, and navicular	35
Metatarsal III, greatest length from distal end to ectocuneiform articulation measured on superior surface	85.7
Metatarsal III, transverse diameter at narrowest portion of the shaft	13.8
Metatarsal IV, greatest length from distal end to cuboid articulation measured on superior surface	82
Metatarsal IV, transverse diameter at narrowest portion of shaft	10.5
Metatarsal V, greatest length from distal end to cuboid articulation measured on superior surface	65
Metatarsal V, transverse diameter at narrowest portion of the shaft	8

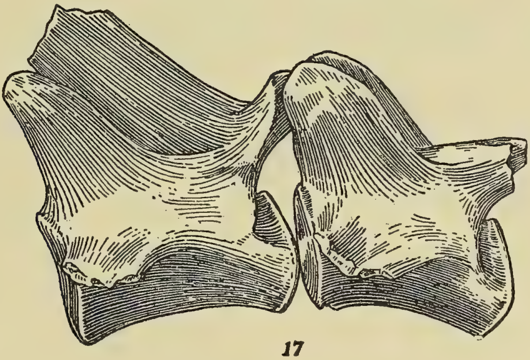
In another specimen, *A. debilis major* (No. 110) showing the same characters as those found in that described above, the perfect tibia and calcaneum have the following dimensions:—

	mm.
Tibia, greatest length	256
Tibia, transverse diameter at proximal end	53
Tibia, antero-posterior diameter at proximal end	55.5
Tibia, transverse diameter at distal end	37
Calcaneum, greatest antero-posterior diameter	70

Vertebrae.—With the *Archaelurus* skull No. 1681 there are preserved the axis and the third cervical. Both are much like the corresponding elements described by Cope for *Nimravus gomphodus*, and no characters are noted which would serve to distinguish them.

Associated with the lower jaw No. 1680, referred to *A. debilis major*, there is in the collections from the Middle John Day a series of four posterior lumbar vertebrae in articulation. The anterior member of the series supports a very sharp, thin, inferior keel, and the metapophyses are narrow. There is a rudimentary anapophysis on this vertebra and the succeeding one. The spine and transverse process are broken away. On the third member of the series (text-figure 17) the inferior keel is strong, but not as thin as on the first, and there is a minute rudiment of an anapophysis on one side only. The neural spine is rather broad and high, but is unfortunately not complete. The fourth vertebra is shorter than the others, the metapophyses are broader, the inferior surface is not distinctly keeled, and the thin transverse processes are well developed though broken distally. This vertebra is peculiar in that it lacks a neural spine. In the place of the spine there is a very indistinct ridge not exceeding a millimeter in height. This last vertebra is presumably the seventh lumbar, the others being the sixth, fifth, and fourth. This vertebra does not agree in form with the seventh lumbar of *Archaelurus debilis* described by Cope, which had a high neural spine.

With the complete tibia and calcaneum, No. 110, referred to *Archaelurus*, there is a large but slender caudal vertebra (text-figure 18) which must have been situated near the middle of a long slender tail.



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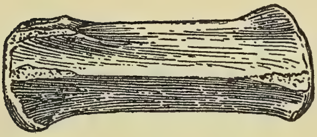

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Fig. 17. *Archaelurus debilis major.* Lumbar vertebrae. No. 1680. Middle John Day, Turtle Cove, John Day Valley, Oregon. × $\frac{3}{4}$.

Fig. 18. *Archaelurus debilis major.* Caudal vertebra. No. 110. Middle John Day, Blue Basin, John Day Valley, Oregon. × $\frac{3}{4}$.

Measurements

	mm.
Vertebrae, associated with type skull of *A. debilis major*, No. 1681	
Axis, length of centrum including odontoid process	53
Axis, antero-posterior length of neural arch, approximate	54
Axis, height from middle of inferior side of centrum to top of neural arch	43
Third cervical, length of inferior side of centrum	22
Third cervical, width across postzygapophyses	33

No. 1680, associated with lower jaw of *A. debilis major* (?)	mm.
Fourth lumbar, length of centrum	40
Fourth lumbar, width of posterior end of centrum	28
Fourth lumbar, height of posterior end of centrum	19
Fifth lumbar, length of centrum	41
Fifth lumbar, width across posterior zygapophyses	24
Sixth lumbar, length of centrum	40.5
Sixth lumbar, width of posterior end of centrum	29
Sixth lumbar, height of posterior end of centrum	19
Sixth lumbar, height of neural spine above lower side of neural canal, approximate	48
Seventh lumbar, length of centrum	38
Seventh lumbar, width of posterior end of centrum	31
Seventh lumbar, height of posterior end of centrum	19
Seventh lumbar, width across metapophyses	33.5
No. 110, associated with *Archaelurus* type of tibia and calcaneum	
Caudal, length	53
Caudal, transverse diameter at narrowest point	14.7
Caudal, height of posterior end of centrum	15

POGONODON DAVISI, n. sp.

Pl. 6, Figs. 1, 2, and 3

No. 789, Univ. Calif. Col. Vert. Palae. From the Upper John Day, five miles southeast of Monument, Grant County, Oregon.

Distinctive Characters.—Skull large, sagittal crest very high and thin, brain case small. Dentition $^{\underline{3}}$, $^{\underline{1}}$, $^{\underline{3}}$, $^{\underline{1}}$. Third upper incisor relatively large. Upper canines large but not greatly compressed laterally. P^2 very small, one-rooted. P^4 without deuterocone, with incipient protostyle, not exceeding the superior canine in antero-posterior diameter. M^1 small, narrow transversely, without distinct internal or protocone lobe.

The type specimen, a skull without mandible, was found in the Upper John Day beds, southeast of Monument, Oregon, by Mr. Leander S. Davis, whose efficient services as guide and collector I take pleasure in recognizing in this connection.

Cranium.—The size of the skull places this form among the larger and more powerful John Day carnivores. The cranium is characterized particularly by the very high and thin sagittal crest, which is so strongly elevated that the highest point on the skull is thrown extraordinarily far back. The brain case is small and the thin crest rises quite abruptly above it. The parietal foramina are situated low down on the base of the crest, but on the left side there is an additional foramen higher up on the side. The occiput is high and narrow, its width a little below the middle being less than that near the upper end. The lower portion is evenly rounded but not keeled, the upper portion is gently concave. A faint median keel and two lateral ones arise near the upper end, but no strong or persistent keel is present on the occiput. The zygomatic arches are widely spread. The root of the zygomatic process of the temporal is not lowered below the level of the basisphenoid as in *Hoplophoneus*. The glenoid fossa is in nearly the same plane with the inferior surface of the basisphenoid, but is not below it, and there is no apparent tendency toward the development of an inferior pedicle for the support of the jaws such as is seen in the typical sabre-tooths. The posttympanic process extends below the plane of the paroccipital process, but is not more strongly produced inferiorly or more closely approximated to the postglenoid than in *Pogonodon brachyops*.

The facial region is flattened and somewhat depressed immediately in front of the orbits, and the nasals are not prominent. The superior extensions of the premaxillaries reach backward a considerable distance, but do not meet the frontals. The nasals extend backward to a point a little behind the narrowest space between the superior margins of the orbits and considerably posterior to the highest point of the maxillaries. Immediately behind the union of the fronto-maxillary and fronto-nasal sutures the nasals are slightly widened. The postorbital processes are prominent and the frontal region is relatively wide. The fronto-maxillary suture extends upward from the border of the orbit and then turns forward nearly horizontally before bending downward to the nasal suture, leaving the frontal with a very small and narrow nasal process. Though not entirely similar, the relations of this suture are somewhat like those of *Deinictis*.

The palate is broad posteriorly and the inferior nares reach forward almost to the molars. The posterior palatine foramina are nearly opposite the anterior border of P^3.

The foramina of the basi-cranial region of the skull are much like those of *Nimravus* and *Deinictis*. The alisphenoid canal and foramen ovale are in a shallow depression near the glenoid fossa. The carotid canal and foramen lacerum posterium appear to be separated.

Dentition.—The anterior ends of the premaxillaries are broken away, leaving only portions of the roots of the incisors. I^1 is small and I^3 very large. The canines are absent, but their alveolar walls are well preserved, giving the approximate dimensions of these teeth at the base. Compared with the sectorials, the antero-posterior diameter is relatively larger than in *Deinictis*, and approaches more nearly the size seen in *Hoplophoneus*. The transverse diameter seems to indicate something less than the degree of compression shown in the canines of most species of *Hoplophoneus*. P^2 was very small and had but one root. P^3 is relatively smaller than in *Deinictis*. In addition to the large posterior cusp, there is present a minute tubercle situated on the inner side of the anterior border. The superior sectorial does not possess a distinct deuterocone, though the inner root is moderately developed. Somewhat above the basal end of the sharp anterior edge of the protocone on the right sectorial there is a faint but distinct notch separating an incipient protostyle. The anterior border of the left sectorial is somewhat worn, but shows traces of a similar notch on the worn edge, though it was evidently weaker than on the other sectorial. Though the incipient protostyle occupies the same position as in *Hoplophoneus* and other more highly specialized sabre-tooths, I do not think that its presence necessarily indicates that this form is to be included in the genus *Hoplophoneus*. In a *Deinictis* specimen (No. 10257) from the White River beds I find similar, though somewhat weaker, notches separating incipient protostyles on P^4 and P^3 of both right and left series.

M^1 is small and is narrow transversely. As in *Nimravus* and *Hoplophoneus*, it is without an inner protocone lobe. There are apparently three closely connate roots, the inner and antero-external being closely united, and the postero-external much reduced.

Systematic Position.—This species differs from all of those previously described from the John Day fauna. Like *Pogonodon platycopis* described by Cope from the John Day, it resembles *Hoplophoneus* in the large size of the canines, and in the reduced P^2 and P^3. It further resembles *Hoplophoneus* in the absence of a deuterocone on P^4, in the tendency to develop a protostyle on this tooth, and in the reduction of the inner lobe of M^1. Excepting the less marked lateral compression of the superior canine, the principal characters of the dentition as known are apparently closer to

Hoplophoneus than to *Deinictis*. Affinities with *Deinictis* are more apparent in the skull characters. The root of the zygomatic process of the squamosal is not produced inferiorly, and the posttympanic process is not extended inferiorly to such an extent as in *Hoplophoneus* and other highly specialized sabre-tooths with long superior canines. The form of the frontals, nasals, fronto-maxillary suture, paroccipital process, posttympanic process and of the root of the zygomatic process of the squamosal all approach the characters seen in *Deinictis*. The very large size of the temporal fossae indicates large temporal muscles, and probably a heavy lower jaw with a large coronoid process as in the *Deinictis* forms.

This species must be considered a very advanced form of the deinictid group, and finds its closest affinities with the two John Day species *platycopis* and *brachyops*, which have been separated from *Deinictis* as a distinct genus, *Pogonodon*, by Cope. It differs from *P. platycopis* considerably in size, in the form and proportions of the posterior portion of the cranial region, and in the form of the narrow M^1. With considerably smaller skull measurements in *P. davisi*, the occiput and sagittal crest are absolutely much higher. As the skull is absolutely much smaller, this difference in the cranial region is evidently not due to sex. The relation of the superior outline of the fronto-facial region and sagittal crest to each other seem also different from the arrangement in *platycopis*, but judgment on this character should probably be suspended, as the frontal region of the type of *platycopis* is imperfect. As far as I am aware, the character of the inner tubercle of the upper sectorial in *platycopis* is unknown. M^1 in *platycopis* is stated by Cope to be characterized by its great transverse extent, while it is exceptionally narrow in *davisi* and *brachyops*.

From *Pogonodon brachyops* it is distinguished by its relatively much larger canine, smaller P^3, narrower M^1, less abbreviated muzzle, and higher sagittal crest.

The species of the deinictid group in the John Day beds include two types. One is represented by *Deinictis cyclops*, which corresponds quite closely in nearly all of its characters to the typical *Deinictis* of the White River. The other group is represented by *davisi*, *brachyops* and *platycopis*. The second group seems to belong pretty definitely with the deinictids, but represents such a degree of advance away from the typical *Deinictis* that it becomes important to refer to it as a distinct division. These species are characterized particularly by increase in the size of the canines, though not to a great extent in the vertical length, reduction of the anterior premolars, loss of M_2 and of the metaconid of M_1, and reduction of the inner lobe of M^1 in two species. In the only species in which the inner side of the superior carnassial has been examined, the deuterocone is reduced. In all three of the species the frontal region seems to be wide, the temporal fossae are exceptionally large, and the auditory meatus is appreciably narrowed by the post-tympanic process. The species thus grouped seem to resemble each other more closely than they do other forms, and stand in decided contrast in most characters to *Deinictis cyclops* of the same beds.

In order to express in the classification the relation of these John Day species to each other and to the typical deinictids of the Oligocene, it seems to me advisable to use the arrangement proposed by Cope, and to separate *platycopis*, *brachyops*, and *davisi* as the *Pogonodon* group, of at least subgeneric rank.

Of the extremities of the Pogonodons very little is known, but Cope has shown that the limbs were slender and the feet narrowed as in the running types seen in *Nimravus* and *Deinictis*.

MEASUREMENTS

	mm.
Length of skull, anterior side of upper canine to posterior side of occipital condyles	197
Length from postorbital process to inion	117
Width across zygomatic arches	157
Width across postorbital processes	84.5
Least diameter above orbits	55.5
Height of inion above foramen magnum	55
Width of occiput at middle	36.5
Height of sagittal crest above parietal foramen	39
Width of palate between upper canines	30
Width of palate between deuterocones of sectorials	50
Length, posterior side C to posterior side M^1	58.5
Length, anterior side P^3 to posterior side M^1	39
Superior canine, antero-posterior diameter of alveolus	23
Superior canine, transverse diameter of alveolus	12
I^2, transverse diameter of alveolus	*a*5
I^3, transverse diameter of alveolus	*a*8.2
P^2, antero-posterior diameter of alveolus	4
P^3, antero-posterior diameter	14.5
P^4, antero-posterior diameter	23
P^4, transverse diameter across deuterocone	11.75
M^1, antero-posterior diameter	6
M^1, transverse diameter	6.5

AGE AND STAGE OF EVOLUTION OF THE JOHN DAY CARNIVORE FAUNA

Canidae.—Compared with the canids of other Tertiary faunas in America, the John Day dogs represent a stage of evolution which does not correspond closely to that of any other formation. The time relations of the genera are shown in the following table:—

	White River	John Day	Mascall and Deep River	Loup Fork
Daphaenus	x	....	....	....
Paradaphaenus	....	x	....	....
Cynodictis	x	x (?)	....	....
Nothocyon	....	x	....	....
Protemnocyon	x	....	....	....
Mesocyon	....	x	....	....
Cynodesmus	....	....	x	....
Temnocyon	....	x	....	....
Tephrocyon	....	....	x	....
Aelurodon	....	....	....	x
Canis	....	....	x (?)	x (?)
Enhydrocyon	....	x	....	....
Philotrox	....	x	....	....
Hyaenocyon	....	x	....	....
Oligobunis	....	x	....	....
Proamphicyon	x	....	....	....
Amphicyon	....	....	....	x
Dinocyon	....	....	....	x
Ischyrocyon	....	....	....	x
Cynarctus	....	....	....	x

Of the nine generic types of canids in the John Day fauna, only one, *Cynodictis*, is considered identical with a White River genus. The John Day form of *Cynodictis* has generally passed under the same specific name as that of the White River beds, but is distinguished from the latter by several characters. The brain case is larger and the teeth are in some respects more specialized. As a whole the type is more advanced than the White River species.

The genus *Paradaphaenus*, while not distantly removed from *Daphaenus* of the White River in some characters, is in many ways more advanced. The inner lobes of the upper molars are broad, with well-developed hypocone. Intermediate tubercles are also present on the crushing face. The brain case is relatively much larger in the John Day form.

The other John Day representatives of the Canidae are all generically quite distinct from any forms found in the White River.

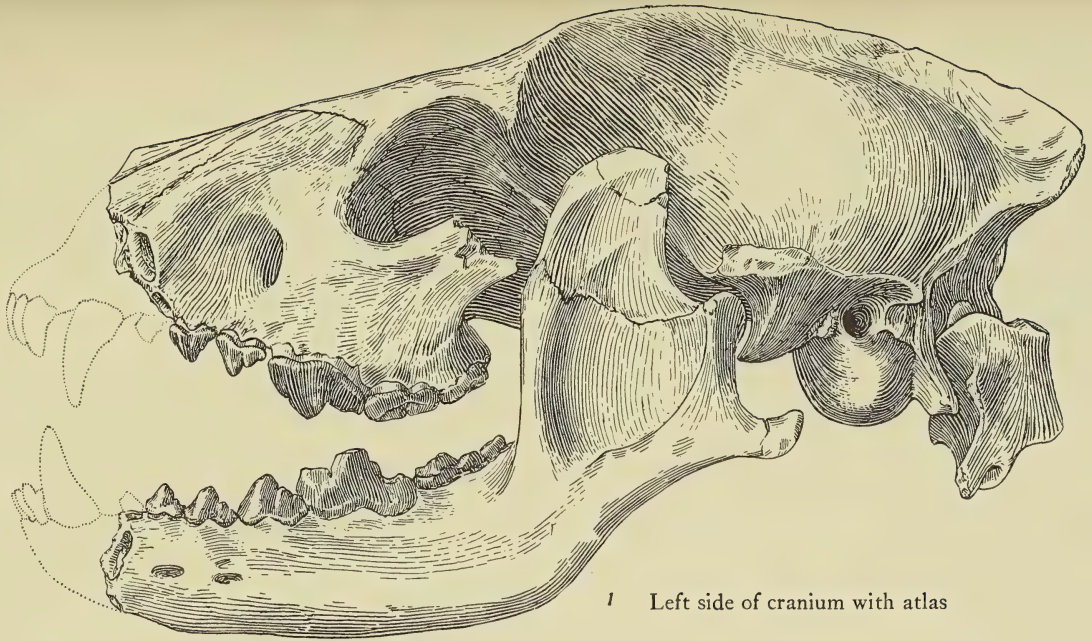
As suggested by several writers, many of the John Day genera represent advances along lines of specialization laid down in the White River epoch. In *Temnocyon*, the cutting function of the lower molars is a little more strongly expressed than the decided tendency in this direction already shown in one form of the White River *Daphaenus*. *Mesocyon* represents an advance over the *Daphaenus* type in the better development of the shear of the lower sectorial, and the partial reduction of the inner tubercle of the heel.

The three species referred to *Nothocyon* are closely related if not generically identical with the John Day *Cynodictis* (?). There can be hardly any question that the Nothocyons are a modification of this stock in which the upper carnassials have been shortened, the molars have approximated the quadrate crushing type, and the brain case has become extraordinarily large. This group is considerably advanced beyond the stage of development of the nearest forms in the White River.

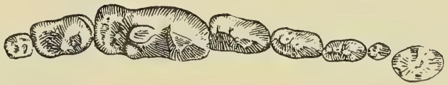
The four remaining canid genera are generally referred to the simocyonine division of the Canidae, having its typical representative in the European *Simocyon*. They are all, as far as known, short-headed forms with heavy jaws and a more or less reduced dentition. While a reasonable doubt exists as to whether these genera are really closely related to the Simocyonines, they are all of a more specialized stage of development than the White River dogs. In some cases there seems to be good reason for believing that they are the more highly specialized descendants of White River forms.

The Loup Fork Canidae are characterized by the presence of the peculiar *Aelurodon* group; by several more or less bear-like genera of the amphicyonine type, *viz.*: *Amphicyon*, *Dinocyon*, *Ischyrocyon*, and *Cynarctus;* and by a few imperfectly known species closely resembling *Canis*. These groups all differ from the John Day dogs and, excepting possibly the case of *Canis*, there is apparently little direct connection to be traced. Even *Canis* is not to be definitely connected with any of the John Day genera. *Mesocyon* may not be far from its ancestral line, but stands rather as the representative of a type than as the ancestor itself.

One of the earliest forms which seems to lead toward the some-



1 Left side of cranium with atlas



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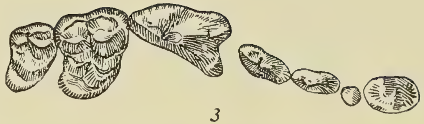
Superior aspect of left inferior dental series



3

Inferior aspect of right superior dental series

Tephrocyon rurestris Condon

From the Mascall beds at Cottonwood, John Day Valley, Oregon

All figures three-fourths natural size

EXPLANATION OF PLATE 2

Fig. 1. *Nothocyon geismarianus mollis*, n. var. No. 90. Middle John Day, Turtle Cove, John Day Valley, Oregon. × $\frac{3}{4}$.

Fig. 2. *Nothocyon lemur* Cope (?). No. 10208. John Day beds, Logan Butte, Crook County, Oregon. × $\frac{3}{4}$.

Fig. 3. *Nothocyon lemur* Cope (?). Natural cast of the brain case from above. No. 10209. Middle John Day, Blue Basin, Turtle Cove, John Day Valley, Oregon. × $\frac{3}{4}$.

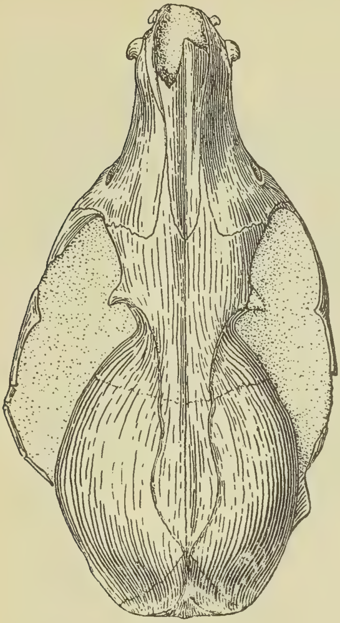
Fig. 4. *Cynodictis* (*?*) *oregonensis*, n. sp. Outer side of left ramus of mandible. No. 316. Middle John Day, Blue Basin, Turtle Cove, John Day Valley, Oregon. × 1.

Fig. 5. *Cynodictis* (*?*) *oregonensis*, n. sp. Superior aspect of right M_1. No. 365. Middle John Day, below Clarno's Ferry, John Day River, Oregon. × 2.

Fig. 6. *Nothocyon latidens* Cope (?). Outer side of left M_1. No. 88. Middle John Day, Turtle Cove, John Day Valley, Oregon. × 2.

Fig. 7. Superior aspect of specimen No. 88 shown in fig. 6. × 2.

Fig. 8. *Nothocyon lemur* Cope (?). Inferior aspect of left superior P^4, M^1, and M^2. No. 1104. Middle John Day, Rudio Creek, Grant County, Oregon. × 2.



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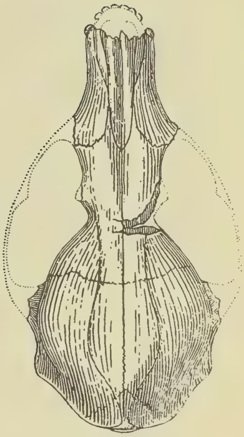

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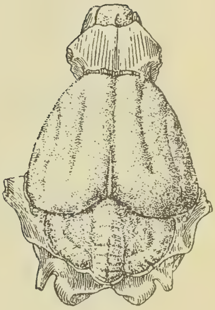

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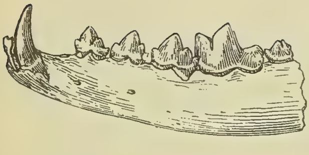

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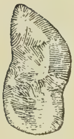

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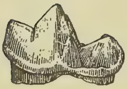

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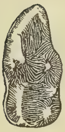

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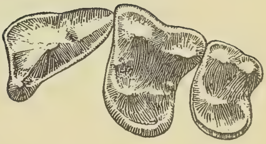

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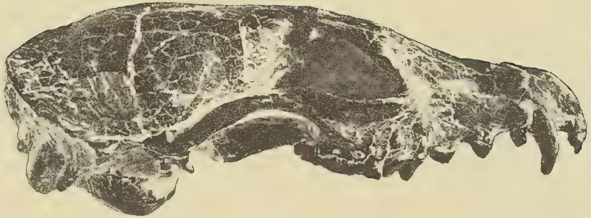

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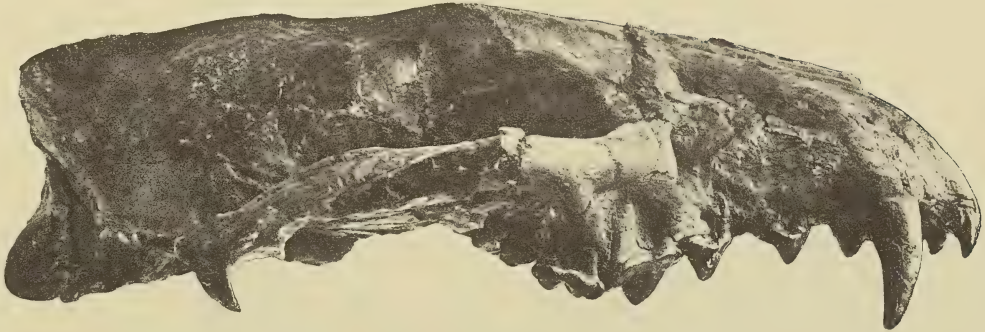

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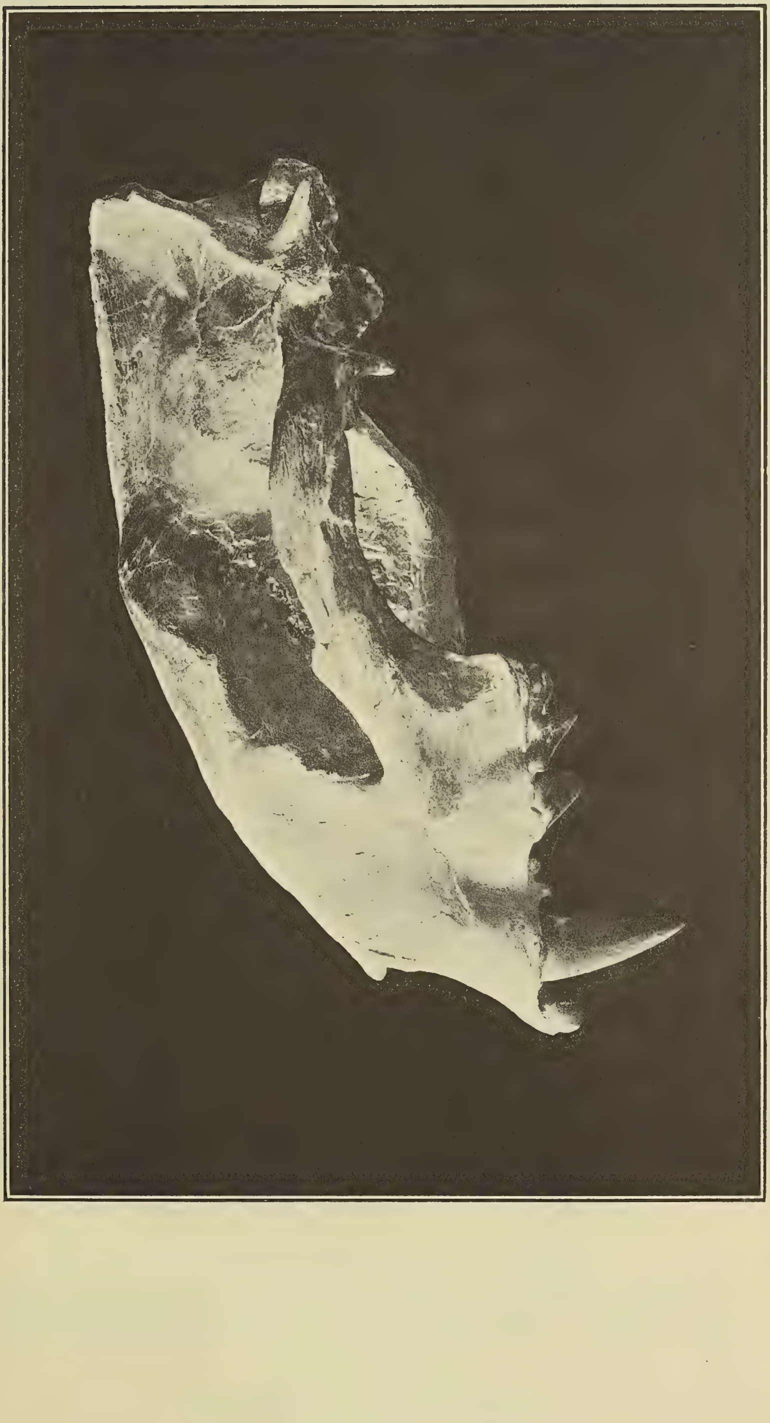
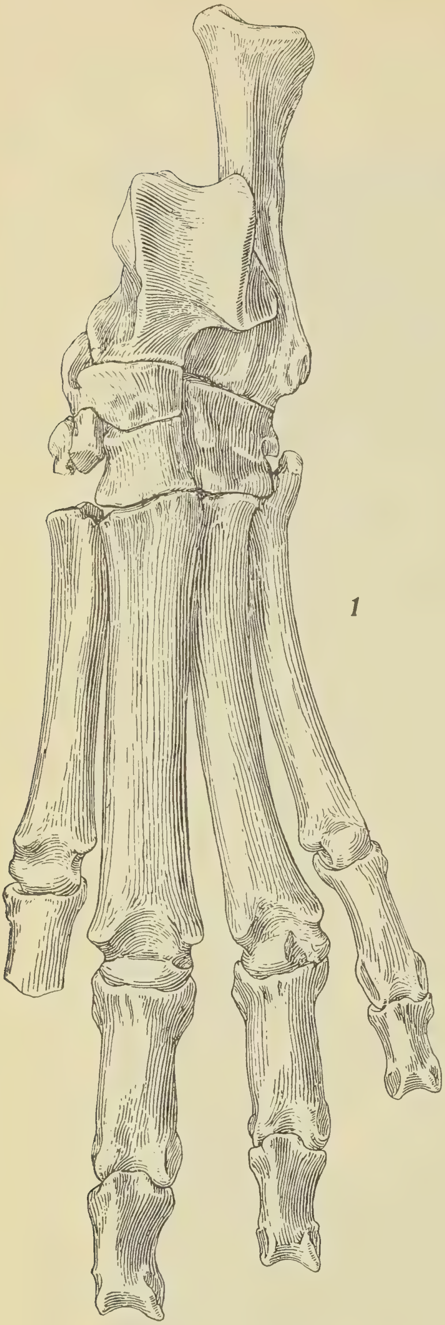
Fig. 1. *Nothocyon geismarianus mollis*, n. var. No. 90. Middle John Day, Turtle Cove, John Day Valley, Oregon. × .73

Fig. 2. *Temnocyon altigenis* Cope. No. 9999. Middle John Day (?), Logan Butte, Crook County, Oregon. × .71



Archaelurus debilis major, n. var. No. 1681. Middle John Day, Logan Butte, Crook County, Oregon. × .53



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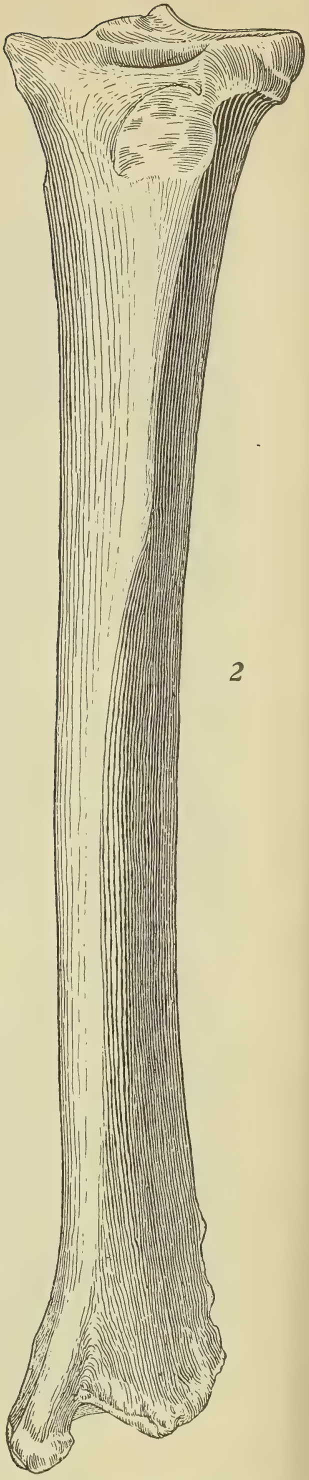


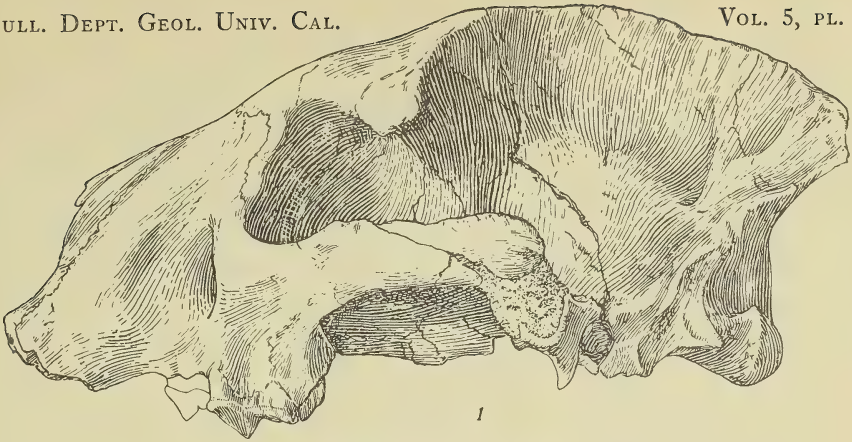
2

Archaelurus debilis major, n. var.

Figures three-fourths natural size

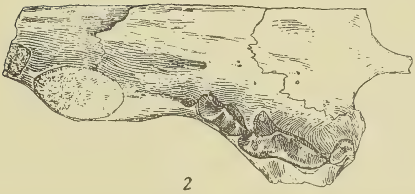
FIG. 1. Left pes. No. 2256. Middle John Day, Logan Butte, Crook County, Oregon.

FIG. 2. Right tibia. No. 110. Middle John Day, Blue Basin, Turtle Cove, John Day Valley, Oregon.



1

Side view of skull No. 789. × ½



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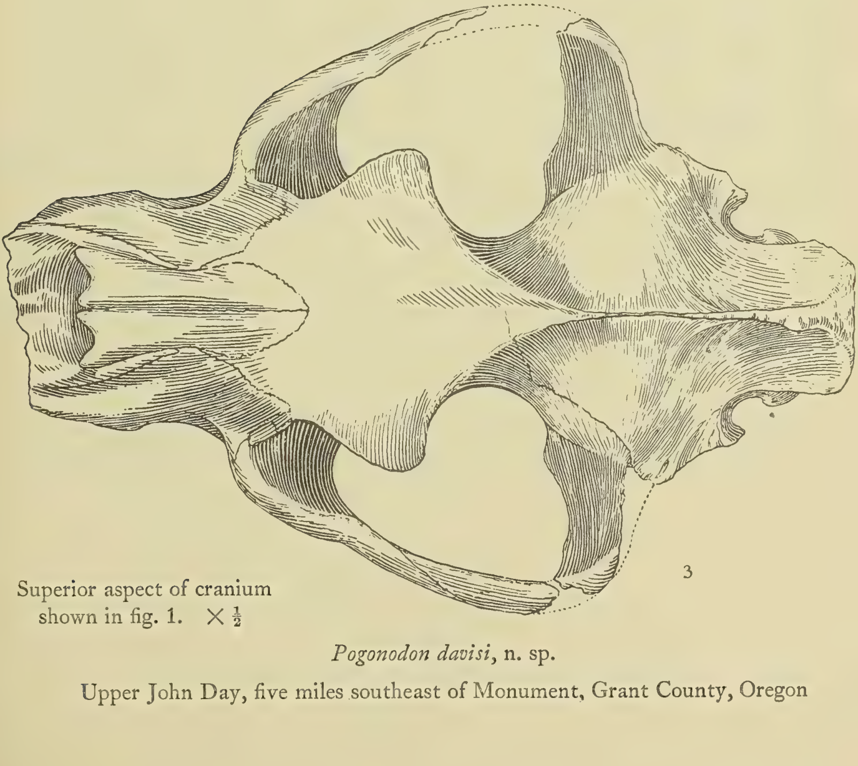
Inferior aspect of palatal region. No. 789 shown in fig. 1. × ½



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Superior aspect of cranium
shown in fig. 1. × ½

Pogonodon davisi, n. sp.

Upper John Day, five miles southeast of Monument, Grant County, Oregon

what specialized Aelurodons is *Tephrocyon* of the Mascall. *Tephrocyon* may possibly be derived from a Mesocyon-like type of the John Day. The amphicyonine canids of Loup Fork represent a branch of the family not known in the John Day and White River. A satisfactory statement of the relative stages of evolution reached in these divisions is difficult, as they are so different, but the degree of advance exhibited by the Loup Fork fauna is on the whole greater. In the *Canis* type an additional factor is introduced, as the Loup Fork species referred to *Canis* appear to be closer to a recent genus than to any John Day form.

In comparison with the Deep River beds, generally considered as older than the Loup Fork and near the age of the upper portion of the John Day, there is but little material from which to draw conclusions. The genus *Cynodesmus* is near *Mesocyon* in most of its characters. The Deep River species referred to *Canis* point toward a later period than John Day.

Fortunately the position of the Tertiary deposits of Eastern Oregon is not dependent on the relationships of the John Day fauna alone. The stratigraphic relations of the Mascall beds to the John Day are well known, and in the Mascall valuable canid remains have been obtained. The physical history of the region shows the Mascall to be separated from the John Day by at least one period of erosion and by the epoch of the accumulation of the Columbia Lava. The best known canid from these beds, *Tephrocyon*, is in many respects similar to *Canis*, but differs in other characters, and is in general a more primitive form than *Canis*. In still other characters it points toward the *Aelurodon* group. It may be near the ancestors of *Aelurodon*, and therefore probably older than the Loup Fork. The relationships of the Mascall Canidae, and the stratigraphic relations taken together indicate that the epoch of the Mascall beds is not far from that of the Deep River. The position of the John Day below these beds puts it into a division much earlier than the Loup Fork.

Felidae.—Remains of representatives of the Felidae are known in Eastern Oregon only from the John Day beds. The relation of these forms to those of the White River and Loup Fork are shown in the following table. The number of species is indicated for each genus.

	White River	John Day	Loup Fork
Deinictis	4	1	....
Pogonodon	....	3	....
Nimravus and *Archaelurus*	....	3	....
Hoplophoneus	6	2	....
Eusmilus	1	....	....
Machaerodus	....	....	1 (?)
Pseudaelurus	....	....	1
Felis	....	....	2 (?)

Compared with the White River cats, the Felidae of the John Day have sometimes been considered the more primitive, having fewer specialized forms of the *Hoplophoneus* type, no *Eusmilus*, almost as many of the deinictids, and the larger part of the whole representation of the family made up of the apparently very primitive forms of the *Nimravus-Archaelurus* group.

In the two genera, common to the John Day and White River, the John Day species are relatively specialized forms. *Hoplophoneus cerebralis*, and the doubtful *H. strigidens* of the John Day are not less specialized than the White River forms, and in some characters show an advance. Of the *Deinictis* group the single typical species, *D. cyclops*, has more slender superior canines than the White River species, and the mandible is relatively slender. The upper sectorial is characterized by the large size and prominence of the deuterocone. The brain case is said by Cope to be rather large.

The three deinictids separated as *Pogonodon* show advance beyond the White River *Deinictis* in their larger size, heavier canines; reduced M^1; loss of M_2, of metaconid of M_1, and of deuterocone of P^4; reduced premolars; and probably in foot structure also, although this is as yet very imperfectly known.

The remaining forms, which are included in the *Nimravus-Archaelurus* group, have appeared to represent more primitive types than any of the White River felines, and being the dominant type of the John Day fauna, their presence has naturally tended somewhat to unsettle conclusions as to the stage of evolution and age of these beds which have been drawn from other evidence. As has been shown under the discussion of *Archaelurus* and *Nimravus*, the forms of this group, while possessing a somewhat primitive dentition, show in it some marks of advance not seen in the nearest White River forms. Moreover, we do not find associated with this apparently primitive dentition the primitive type of extremity which should accompany it if this were an especially low or early stage in the evolution of the group. The limbs are relatively long and slender and indicate development of speed rather than prehension, as in the hunting leopard. We should therefore expect to find that in *Archaelurus*, as in the living hunting leopard (*Cynaelurus*), specialization of the feet for running, with weaker prehension, would be correlated with short canines; and that the cheek teeth, having more work to perform in holding and killing prey, would be less reduced, and would be more efficient weapons.

Compared with the genus *Deinictis*, which also possessed rather slender limbs with an apparently primitive dentition, *Archaelurus* shows greater reduction of the lateral digits in the posterior limb, and a relatively longer metapodial region. In dentition and skull *Archaelurus* is more primitive than *Deinictis* in the frequent possession of a very small P^1, in the lack of inferior projection of the posttympanic process and of the root of the zygomatic process of the temporal, and in the absence of a flange on the lower jaw. The latter character is associated apparently with less pronounced elongation and lateral compression of the upper canines. *Archaelurus* is, however, more specialized than the typical *Deinictis* in lacking a metaconid on M_1; in the reduction of the deuterocone of P^4, and of the inner lobe and root of M^1; and in the possession of the peculiar exostoses on the mandibular rami. On the whole, it does not appear that the dentition in the *Nimravus-Archaelurus* group is less specialized than that in *Deinictis*. In the loss of the inner tubercles on both upper and lower carnassials and on the upper molar it certainly shows a distinctly advanced type.

Though *Archaelurus* has been considered by many as the type ancestral to *Deinictis*, there seems to be no good reason for supposing such a relationship to have existed, particularly as the evidence indicates that *Archaelurus* flourished in association with the most advanced members of the deinictid group. While in some of the characters which distinguish the true sabre-tooths *Archaelurus* is nearer the primitive cats than *Deinictis*, the same may be said of *Felis*. Just as in *Felis*, though to a less extent, the line of development of *Archaelurus* may have taken a different direction from that in the true sabre-tooths and the emphasis have been put on other features.

The apparent near kinship of the *Nimravus-Archaelurus* forms with *Ailurictis* occurring in the lower Oligocene of Europe is sometimes advanced as strong evidence of antiquity of the John Day fauna. Our present knowledge of this group seems to indicate an Old World origin of these American John Day genera, but the American species are somewhat more advanced in reduction of the lateral digits, and possibly in the reduction of the deuterocone of P^4. The exostosis of the mandible may also indicate a more specialized stage. If *A. sivalensis*, of the Indian Siwaliks, is a member of this group, the genus must have been strongly persistent, and its occurrence in the John Day would not necessarily indicate Oligocene age.

In the Loup Fork, the species of true *Felis* and of *Machaerodus* represent a more advanced stage of development and a closer approximation to the recent fauna than is found in either the John Day or White River.

Conclusions.—Taken together, the Canidae and Felidae of the John Day represent a stage of evolution somewhat more advanced than that reached in the White River and less advanced than that of the Loup Fork. Compared with the known faunas of Europe, they appear to be not older than the middle Oligocene of Fontainbleau and not as young as the middle Miocene of Sansan.

Issued November 30, 1906

TERTIARY FAUNAS OF THE JOHN DAY REGION

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Introduction

In several publications appearing at intervals since 1901 there have been presented the principal geological and palaeontological results obtained by the University of California expeditions in the John Day region of Oregon. A general statement of the results so far as correlation and faunal relations are concerned has, however, been deferred until all of the available evidence should be obtained from the several fields of investigation in which work has been in progress. The following contribution is based primarily on the collections made by parties from the University of California working in the valley of the John Day River during the summers of 1899, 1900, and 1901, and by Messrs. V. C. Osmont and L. S. Davis, who collected along the John Day and in the Crooked River basin in 1900. Particular attention was paid in the field to the study of the vertical range of species, and it is

By John C. Merriam and William J. Sinclair. *University of California Publications, Bulletin of the Department of Geology*, vol. 5, no. 11, pp. 171–205, October 12, 1907.

now possible to present some account of the time range of a considerable proportion of the Tertiary fauna of this region, and to offer some suggestions regarding the correlatives of the formations containing mammalian remains.

The writers desire to express their indebtedness to Mr. J. W. Gidley, who has studied the horse material collected from the Mascall and Rattlesnake beds. The John Day rhinoceroses in the University of California collection have been submitted to Professor H. F. Osborn for determination, but his report has been delayed, pending a further revision of the group, especially of the later Oligocene and Miocene North American forms.

Stratigraphic Succession of the Cenozoic Formations in the John Day Basin

The stratigraphy of the John Day basin has been discussed in a previous paper.[1] The section there described may be expressed in tabular form as shown on the opposite page.

The oldest formation in the basin affording mammalian remains is the John Day, which overlies the plant-bearing Clarno beds. On stratigraphic and palaeontologic grounds the John Day has been subdivided into three divisions: lower, middle, and upper.[2]

The lower division is composed of red, white, and green tuffaceous shales, which weather down into mud-covered dome-like hills. No unconformity has been observed between this division and the Middle John Day, although it is possible that one exists. The brilliant color of the lower beds, their characteristic lithology, and the almost total absence of fossils separate them sharply from the Middle John Day in which vertebrate remains are abundant.

The rocks of the middle division are andesitic tuffs of a characteristic green or greenish-blue color. Thin flows of rhyolitic lava are interbedded with these tuffs at Bridge Creek and in Turtle Cove.

The upper division is composed of tuffs petrographically similar to those of the Middle John Day but prevailingly light buff in color. At a number of localities sands and gravels are found near the top of the formation, indicating a change in the mode of deposition.

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[1] Merriam, J. C. A Contribution to the Geology of the John Day Basin. Bull. Dept. Geol. Univ. Cal., Vol. 2, pp. 269–314.

[2] Merriam, *Ibid.* pp. 293–295.

Age		Section in the John Day Basin		Correlatives
Quaternary		Terrace deposits with *Equus* and *Elephas* remains.		Later half of Quaternary.
		Erosion interval (tilting of the Rattlesnake and erosion of John Day Cañon).		Sierran (?)
Pliocene		Rattlesnake formation (tuffs, gravels, ashy soil, and rhyolitic lavas).		Not Determined.
		Unconformity (tilting and erosion of the Mascall).		
Miocene	Later Miocene	Mascall formation (tuffs, ashes, and possibly gravels).		Pawnee Creek beds, Colorado; Deep River beds, Montana; Ellensberg formation, Washington[3]
	Earlier Miocene	Columbia Lava (basalt and interstratified basaltic tuffs).		Yakima Basalt, Ellensberg quadrangle, Washington. Harrison formation. Monroe Creek formation. Rosebud formation.
		Unconformity. Slight folding of the John Day. Interval of erosion.		
Oligocene		John Day Series	Upper John Day (mainly buff-tinted tuffs. Sands and gravels near top).	
			Middle John Day (drab and bluish-green tuffs).	
			Lower John Day (red, white and green tuffaceous shales).	
		Unconformity.		
Eocene		Clarno formation (shales, tuffs, andesitic and rhyolitic lavas). The Clarno has yielded an abundant flora but no vertebrate remains have yet been found.	Upper Clarno beds. (Upper Eocene).	Payette formation, Idaho.[4] Manastash formation, Washington.[5]
			Lower Clarno beds. (Lower Eocene).	
		Unconformity.		
Cretaceous (Marine)		Chico formation (sandstones and conglomerates).		Basal Chico at Texas Springs and near Horsetown, California; Phoenix beds at '49 Mines, Oregon.[6]

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[3] Knowlton, F. Fossil Flora of the John Day Basin. U. S. G. S. Bulletin 204, pp. 109–110.

[4] *Ibid.* pp. 110–111.

[5] Smith, G. O. Professional paper U. S. G. S. No. 19, p. 16.

[6] Stanton, T. W. Note in Bull. Dept. Geol. Univ. Cal., Vol. 2, p. 284.

No sharp stratigraphic line can be drawn between the Middle and Upper John Day, the color of the beds usually serving for their discrimination in the field. Faunally, the dividing line between them may be fixed by the downward range of *Promerycochoerus* which is not known to occur in the Middle John Day. This limit is for the present regarded as lying about 100 feet above a prominent stratum of coarse gray tuff exposed quite generally near the top of the Middle John Day in Turtle Cove, where, by differential weathering, it usually forms a terrace. The bluish-tinted tuff beds above this stratum contain a rodent fauna practically identical with that occurring lower down in the Middle John Day and are, accordingly, incorporated with the middle division.

Before the extravasation of the Columbia Lava, the John Day formation was subjected to erosion. The surface thus produced is known to have supported a growth of timber in at least one locality. Partly charred and partly silicified wood has been found at the contact of the buff beds with the lava, numerous sticks and stems extending some distance upward into the lower portion of the lava flow. Angular unconformity has been observed between the lava and the John Day, due to gentle folding of the latter formation previous to the outpouring of the lava.

The Columbia Lava is built up of numerous heavy sheets of olivine basalt with relatively insignificant amounts of basaltic tuffs interbedded with the flows.[7] In Oregon, the lava series reaches a thickness of one to two thousand feet.

Resting on the Columbia Lava without observed unconformity is the Mascall formation. The lower beds, from which numerous leaf impressions and poorly preserved fish remains have been obtained, are described by Calkins as fine-grained, chalky rocks, probably in part of organic origin. Grey friable tuffs composed largely of glass particles also form part of the series. The upper beds which yield the mammalian remains are tuffs of light color, fine grain, and harsh texture. At several localities thin basalt flows are interstratified with the lower Mascall beds.

Upon the uptilted and eroded edges of the Mascall there lies a considerable thickness of gravel, tuff and rhyolitic lava which has been named the Rattlesnake formation, from its typical occurrence on Rattlesnake Creek near Cottonwood. The basal gravels of the

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[7] Calkins, F. C. A Contribution to the Petrography of the John Day Basin. Bull. Dept. Geol. Univ. Cal., Vol. 2, p. 159.

Rattlesnake contain many pebbles evidently derived from the Columbia Lava. Vertebrate remains have been obtained from both the tuffs and the gravels.

The tuffaceous layers are irregularly bedded but appear to have been worked over by wind, and to have formed soil or dirt beds supporting a considerable growth of plants. In some places they are filled with slender cord-like bodies which evidently represent mineral accumulation about small roots. Along one section of a soil bed a large number of fragments of horse bones and teeth, evidently all belonging to one individual, were scattered for a horizontal distance of over twenty feet and through one and one-half feet in thickness. The scattered and broken condition of the bones of this individual seems to indicate a long exposure of the remains on a land surface which was being rapidly worked over.

In some sections the prominent rhyolitic bed forms the cap of extensive tables. In other regions, as near Belshaw's ranch, there are at least two hundred feet of gravels above the rhyolite bed.

The close of Rattlesnake deposition marks the beginning of an interval of erosion which may be regarded as the opening event of the Quaternary. It has been suggested that the deformation of the Rattlesnake occurred after the John Day River had established itself in its present course.[8]

Stream terraces are found along the John Day and its main branches, and there are many old alluvial slopes covered with angular rubble. Remains of *Elephas* and *Equus* are preserved in the Quaternary terrace gravels.

History of Correlation

The earliest expression of opinion regarding the correlation of the Tertiary formations in the John Day valley seems to have been that of O. C. Marsh[9] in 1875. Of the John Day Marsh wrote: "The typical localities of this Miocene basin are along the John Day River, and this name may very properly be used to designate the lake basin. . . . The upper beds alone of this series correspond to the deposits in the White River basin. The lower portion also is clearly Miocene, as shown by its vertebrate fauna, which differs in many respects from that above." The Clarno is referred to as "the Eocene beds containing fossil plants." The presence of

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[8] Merriam. *Op. cit.*, p. 312.

[9] Am. Jour. Sci. 3d. ser. Vol. 9, p. 52, 1875.

Pliocene beds above the Miocene is also noted. The so-called Pliocene is evidently the Mascall and Rattlesnake, near the typical exposures of which on Cottonwood Creek Marsh is known to have camped.

Views similar to those of Marsh were entertained by Cope[10] who wrote of "the White River beds of the John Day region." In the same paper the Mascall and Rattlesnake are referred to as "the Loup Fork formation of Cottonwood Creek."

By Clarence King[11] the John Day was correlated with the Truckee group, and both formations were supposed to have been deposited in the same body of water, Pah-Ute Lake. In explanation of this correlation King stated that: "The main reason for classing the whole group" (*i.e.*, Truckee) "as Miocene is that farther north in Oregon, upon John Day, Des Chutes and Crooked Rivers, Professor Marsh's researches have brought to light an immense formation, computed by him to be 3000 or 4000 feet thick, containing numerous vertebrate remains of clearly Miocene type. These Oregon beds are all in inclined position, earlier than basaltic eruptions, and the main material of his whole series, as I have determined by microscopic studies, is of stratified trachytic pumice, tuffs and hyaline sands. The Oregon Miocene is apparently the direct northward continuation of the Nevada formation. Besides the parallelism between the two series is the fact of an overlying unconformable Pliocene in each case." It would seem from this reference to the Pliocene that King possibly identified the Mascall or Rattlesnake with the deposits in his Shoshone Lake. On a later page[12] the following table was presented by King:

MIOCENE

Contemporaneous

Province of Nevada and Oregon.	Province of Great Plains.
Pah-Ute Lake (Truckee Group, King; John Day Group, Marsh).	Sioux Lake (White River Group, Hayden).

King's correlation was adopted by Cope[13] in his later writings. In 1880 he published the following general account of the geology of the John Day country: "The regions of the John Day River and Blue Mountains furnish sections of the formations of central Oregon. Above the Loup Fork or Upper Miocene there is a lava outflow, which has furnished the materials of a later lacustrine formation, which contains many vegetable remains. The material is coarse, and sometimes gravelly, and it is found on the Columbia River and I think also in the interior basin. Professor Condon, in his unpublished notes, calls this the Dalles Group. It is in turn overlaid by the beds of the second great volcanic outflow. Below the Loup Fork follows the Truckee Group, so rich in extinct mammalia, and below this a formation of shales. These are composed of fine material, and vary in color from a white to a pale brown and reddish-brown. They contain vegetable remains in excellent preservation, and undeterminable fishes.

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[10] Observations on the Faunae of the Miocene Tertiaries of Oregon. Bull. U. S. Geol. Surv. of the Terrs., Vol. 5, Article 3, 1879.

[11] U. S. Geol. Exploration of the Fortieth Parallel, Vol. 1, p. 423.

[12] King. *Op. cit.*, p. 458.

[13] Proc. Am. Phil. Soc., p. 61, 1880.

"The *Taxodium* nearly resembles that from the shales at Osino, Nevada, and on various grounds I suspect that these beds form a part of the Amyzon Group (American Naturalist, June, 1880), with the shales of Osino and of the South Park of Colorado. Below these is a system of fine-grained sometimes shaly rocks of delicate gray, buff and greenish colors, containing calamites, which Professor Condon calls the Calamite beds. Their age is undetermined."

In his monograph on the Tertiary Vertebrata, Cope[14] writes of the White River and John Day: "The eastern area of this formation is the true White River epoch of Hayden; the western deposits form the Truckee epoch of King. I named this formation the Oregon, but Mr. King's name is the older and must be retained.

"According to Professor Condon, the Truckee formation of Oregon, on the John Day River, rests unconformably on the laminated beds containing *Taxodium* and fish remains, which, as I have suggested on a previous page, may be an extension of the Amyzon shales. These in turn rest on a formation of hard laminated beds, which contain an abundance of calamites, which doubtless belong to the Triassic or Jurassic period. The Truckee beds are, like the true White River, overlaid by the Loup Fork, and this in turn by heavy beds of basalt."

The beds at Van Horn's ranch containing fish remains, which Cope assumed were to be correlated with the Amyzon group, were referred by Lesquereux[15] to the late Miocene and are now known as the Mascall formation. The Calamite beds were placed by Lesquereux in the Eocene and are undoubtedly the Clarno. Cope's error in correlating the beds containing the fish remains with the Amyzon group arose from confusing the Mascall with the Clarno.

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[14] U. S. G. S. of the Terrs. Report, Vol. 3, p. 15.

In the monograph referred to above,[16] Cope proposes the following table of equivalent European and American horizons:

West Europe			North America	
Oeningian	Oeningian	Tertiary	Loup Fork	Procamelus beds
Tortonian	Falunian			Ticholeptus beds
Langhian			White River	Truckee
Aquitanian	Aquitanian			White River
Stampian	Tongrian			

The term Truckee was later abandoned by him in favor of Marsh's John Day. The change in nomenclature appears in a note on the vertebrate fauna of the Ticholeptus beds published in 1886.[17]

"In the Report of the U. S. Geological Survey of the Terrs., Vol. III. p. 18 (1884), I have given some of the characters of this horizon" (*i.e.*, the Ticholeptus beds) "and its fauna. It is intermediate in all respects between the Middle and Upper Miocene formations of the West, as represented by the John Day and Loup Fork beds. It was first explored in the valley of Deep River, Montana, by my assistant, J. C. Isaac, and afterwards by J. L. Wortman on the Cottonwood Creek, Oregon. At the latter locality it is seen to rest on the John Day beds, as stated by Mr. Wortman, and is indicated by the collections made by him." The statement regarding the superposition of the so-called Ticholeptus beds on the John Day should probably be read as "above" rather than "on the John Day." This formation has been termed the Cottonwood beds,[18] Loup Fork beds, Amyzon beds[19] and Protolabis beds.[20] In Oregon it is now known as the Mascall formation.

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[15] Proc. U. S. National Mus., Vol. 11, p. 13, 1889.

[16] Tertiary Vertebrata, table opposite p. 43.

[17] Am. Nat., Vol. 20, pp. 367–368, 1886.

[18] Bull. Am. Museum of Nat. Hist., Vol. 12, p. 23; also Jour. of Geol., Vol. 9, p. 72.

[19] Cope. Proc. Am. Phil. Soc., 1880, Vol. 19, p. 61.

[20] Wortman. Bull. Am. Mus. Nat. Hist., Vol. 10, pp. 120, 141.

Cope's correlation of the Mascall with the Montana Deep River is rejected by Scott,[21] as follows: "I cannot agree with Cope in regarding the strata of western Nebrasca and Cottonwood Creek, Oregon, as referable to the same horizon as those of the Deep River valley in Montana. . . . The reference of the beds developed along Cottonwood Creek and the upper John Day River, in Oregon, to the Deep River horizon, is determined by the occurrence in them of a so-called *Anchitherium* and of a species identified as *Blastomeryx borealis*. It should be noted, however, that the term *Anchitherium* is used in the sense of *Miohippus*, the species from Montana which I have called *A. equinum* is a very different animal and belongs to the group of *A. aurelianense*, of Europe, which it equals in size. *Miohippus* is found in the typical Loup Fork, as well as in the lower series (see Osborn, Bull. Mus. Comp. Zool. Cambridge, Vol. 16, p. 89, under the title *Anchitherium parvulum*). No great weight therefore, can be attached to the occurrence of the genus in the Cottonwood Creek beds. The presence of *Blastomeryx borealis* would, of itself, be insufficient for the correlation of the two localities, but the identification of the species is not at all certain. Besides certain minor differences in the teeth, the limb bones from the Oregon beds indicate the existence there of two species, both of which are much heavier than the Montana forms and are more like others from the Loup Fork of Kansas."

In the same paper[22] the lower strata in the valley of Deep River are referred to the top of the John Day.

Certain "deposits of gravel, clay and volcanic dust" lying above the lavas of the Columbia River in eastern Washington have been correlated by Russell[23] with the John Day. "Beds of light-colored clay and of white volcanic dust, which have been referred to the John Day system, occur at the White Bluffs of the Columbia, 30 miles above Pasco, and are also well exposed in Naches Valley and near Ellensberg in Yakima County." Knowlton[24] has shown that the leaf-bearing beds above the lava in the vicinity of Ellensberg are the correlatives of the Mascall.

Scott[25] has formulated his views regarding the European equivalents of the White River and John Day in an address delivered before the British Association for the Advancement of Science from which the following extract is taken:

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[21] The Mammalia of the Deep River Beds. Trans. Am. Phil. Soc., Vol. 17, p. 60, 1893.

[22] Scott. *Op. cit.*, p. 60.

[23] Reconnaissance in Southeastern Washington, U. S. G. S. Water Supply and Irrigation Papers, No. 4, 1897.

[24] Ellensberg Folio, U. S. Geol. Atlas, note in descriptive text.

[25] Rept. Brit. Ass. for the Adv. of Sci., 1895, p. 681.

"The White River is Oligocene (Ronzon) and much misunderstanding has come from calling it Miocene. The John Day may be placed in the Lower Miocene, though it is somewhat older than the beds at St. Gerand-le-Puy, and follows the White River with hardly a break. None of the American lacustrines is referable to the Middle Miocene. The Loup Fork is Upper Miocene, the Deep River division corresponding almost exactly to the beds at Sansan and Steinheim. . . ."

By Von Zittel[26] the John Day has been placed as the equivalent of the beds at Sansan and Steinheim. The so-called Ticholeptus beds of Cottonwood Creek, Oregon, are correlated with the sands of Eppelsheim and the beds at Pikermi near Athens and Maragha in Persia. The beds at St. Gerand-le-Puy and Ronzon are correlated with the White River, which is referred in part to the Miocene and in part to the Oligocene, while the John Day is called Middle Miocene and the Ticholeptus beds Upper Miocene.

In an extensive correlation table, W. H. Dall[27] has bracketed opposite each of the formations in question what he regards as their equivalents in various parts of the United States, and also the corresponding European horizons. The Oligocene is here admitted as a fourth division of the Tertiary. A part of the table is herewith reproduced:

A	EPOCHS AND STAGES	B	PACIFIC COAST	C	LAKE BEDS	F	FOREIGN
4	Miocene	9	Ione formation				
		10	Sooke beds				
		11	Empire beds	4	Loup Fork		
		12	Astoria sandstone			5	Helvetian
		13	Monterey beds	....	....		
5	*Transitional*	....	....	5	Deep River	6	Sansan beds
	Oligocene						
6	*a.* Upper or Chipolan	14	Tunnel Point beds (?)	6	John Day	7	Aquitanian
		15	Astoria shales				
7	*Transitional*	....	....	7	Protoceras bed	8	Tongrian
	b. Lower or			8	White River Upper		
8	Vicksburgian	16	Aturia bed	9	Middle		
				10	Lower	9	Ligurian

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[26] Handbuch der Palaeontologie, Band 4, s. 65–66.

[27] Eighteenth Annual Report, U. S. G. S., Part 2, table opposite p. 334.

W. D. Matthew[28] has suggested as probable an "overlap to some extent" of the Protoceras beds on "the Lower Miocene John Day." "The Cottonwood basin, containing a higher fauna," is made "equivalent to the Deep River (Cope and Wortman) or Loup Fork (Scott)." In the correlation table published by Matthew,[29] the Diceratherium beds[30] of the John Day and a portion of the Promerycochoerus beds[30] are made the equivalent of Horizon C of the Colorado White River section, which is referred in part to the Oligocene and in part to the Lower Miocene. The Rattlesnake is spoken of as "the loose gravels overlying the Cottonwood beds" and is placed above the Loup Fork and referred to the Pliocene. In a later paper Matthew[31] has called the Diceratherium beds Upper Oligocene and the Promerycochoerus beds Lower Miocene. The Mascall is placed in the Middle Miocene. As the latter reference is framed in accordance with the four-fold subdivision of the Tertiary, it is, perhaps, less discordant with Knowlton's[32] views regarding the Upper Miocene age of the Mascall than would at first appear.

The following table of European and American equivalents has been published by Osborn:[33]

Miocene	Upper	Tortonien		Loup Fork
	Middle	Helvetien		Lower Loup Fork and
	Lower	Langhien		Upper John Day
Oligocene	Upper	Aquitanien		Lower John Day (Diceratherium beds)
	Lower	Tongrien	Stampien Infra-Tongrien	White River

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[28] A Provisional Classification of the Fresh-Water Tertiary of the West. Bull. Am. Mus. Nat. Hist., Vol. 12, Article 3.

[29] *Ibid.*, p. 23.

[30] See under heading: The John Day, *Palaeontological classification.*

[31] Notice of Two New Oligocene Camels. Bull. Am. Mus., Vol. 20, p. 214, 1904.

[32] Bulletin U. S. G. S., No. 204, p. 108.

[33] Correlation Between Tertiary Mammal Horizons of Europe and America, with Third Trial Sheet, Annals N. Y. Acad. Sci., Vol. 13, pp. 1–72, 1900.

The Geological and Faunal Relations of Europe and America During the Tertiary Period and the Theory of the Successive Invasions of an African Fauna. Science, n. s., Vol. 11, p. 561, 1900.

See also Osborn, Bull. Am. Mus. Vol. 23, pp. 237–253, 1907, issued since the preparation of present article. The Lower John Day is placed in the second phase of the Middle Oligocene, equivalent to the Leptauchenia beds and Protoceras sandstones. The Middle John Day is referred to the Upper Oligocene, and is believed to be closely equivalent faunally to

A still later table is the following by Hatcher:[34]

Miocene	Loup Fork	Goodnight = Palo Duro = Ogalalla Nebrasca = Upper Deep River Harrison = Hiatus between Lower and Upper Deep River
	Arikaree	Monroe Creek = Upper John Day and Lower Deep River Gering Sandstone = Lower John Day
Oligocene = White River		Leptauchenia Clays, including Protoceras Sandstones Oreodon Clays, including Metamynodon Sandstones Titanotherium Sandstones and Clays

The reasons which have governed the determinations of geologic age and stratigraphic equivalency expressed in the table on page 541 of the present paper are stated at length in the following chapters:

THE JOHN DAY

Palaeontological Classification.—Two faunas may be recognized in the John Day, corresponding to the middle and upper stratigraphic subdivisions. The Lower John Day will probably prove to be faunally distinct from the beds above, but until its fauna is better known it must be left without a palaeontologic designation.

Wortman[35] has proposed a subdivision of the series into lower or Diceratherium beds and upper or Merycochoerus beds, the former corresponding to the middle and the latter to the upper of the three subdivisions now recognized. The value of the term "Diceratherium beds" is greatly diminished by the difficulty of identifying *Diceratherium* in the field, owing to the usual fragmentary character of much of the rhinoceros material encountered. As yet it is also not altogether certain that the genus is confined to the Middle John Day.

The palaeontological designation of the Upper John Day[36] has varied considerably owing to changes in the generic name of its characteristic oreodont, which has been shown by Matthew[37] and

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the Aquitanien of France (St. Gerand-le-Puy). The Upper John Day is regarded as transitional between Oligocene and Miocene. The Mascall is placed in the earlier Miocene. The Rattlesnake is referred to the Lower and Middle Pliocene.

[34] Proc. Am. Phil. Soc., Vol. 41, p. 118, 1902.

[35] Extinct Camelidae of North America. Bull. Am. Mus. Nat. Hist., Vol. 10, p. 120.

[36] Merycochoerus beds. Wortman. Bull. Am. Mus., Vol. 10, p. 120.

Paracotylops beds. Merriam. Bull. Dept. Geol. Univ. Cal., Vol. 2, p. 296.

Promerycochoerus beds. Matthew. Memoirs Am. Mus., Vol. 1, pt. 7, legend of fig. 19, p. 399.

[37] Matthew. *Op. cit.*

Douglass[38] to belong not to *Merycochoerus* but to a distinct genus named by the latter *Promerycochoerus*.

It has been suggested[39] that the sands, gravels and tuffs at the top of the Upper John Day may represent a third faunal subdivision. They are typically exposed on Johnson and Bologna Creeks, on Bridge Creek, and in the upper end of Haystack Valley, and are characterized by numerous remains of *Miolabis* (*Paratylopus*). Until the fauna of these beds is better known it may be best to include them with the Promerycochoerus horizon.

The Total Fauna.—For convenience in reference, a complete list of John Day vertebrate species is appended. The list is by no means a final one, and it is to be expected that numerous changes will be made as a complete revision of the fauna progresses.

CARNIVORA

Canidae

Paradaphaenus cuspigerus (Cope)	American Museum*
Paradaphaenus, sp. indesc. (*Amphicyon hartshornianus* in part)	American Museum
Nothocyon geismarianus (Cope)	American Museum
Nothocyon geismarianus mollis Merriam, J. C.	University of California
Nothocyon lemur (Cope)	American Museum
Nothocyon latidens (Cope)	American Museum
Temnocyon altigenis Cope	American Museum
Temnocyon wallovianus Cope	American Museum
Temnocyon ferox Eyerman	Princeton University
Mesocyon coryphaeus (Cope)	American Museum
Mesocyon josephi (Cope)	American Museum
Mesocyon brachyops Merriam, J. C.	University of California
Hyaenocyon basilatus Cope	American Museum
Hyaenocyon sectorius Cope	American Museum
Oligobunis crassivultus Cope	American Museum
Enhydrocyon stenocephalus Cope	American Museum
Philotrox condoni Merriam, J. C.	University of California
Cynodictis (?) *oregonensis* Merriam, J. C.	University of California

Mustelidae

Parictis primaevus Scott	Princeton University

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[38] Douglass. Am. Jour. Sci., 4th ser., Vol. 11, p. 82, 1901.

[39] Sinclair. Jour. of Geology, Vol. 9, p. 706, 1901.

* *Location of type specimen.*

FELIDAE

Dinictis cyclops Cope	American Museum
Archaelurus debilis Cope	American Museum
Archaelurus debilis major Merriam, J. C.	University of California
Nimravus gomphodus Cope	American Museum
Nimravus confertus Cope	American Museum
Pogonodon davisi Merriam, J. C.	University of California
Pogonodon brachyops Cope	American Museum
Pogonodon platycopis Cope	American Museum
Hoplophoneus cerebralis Cope	American Museum
Hoplophoneus strigidens Cope	American Museum

RODENTIA

SCIURIDAE

Sciurus wortmani Cope	American Museum
Sciurus ballovianus Cope	American Museum

HAPLODONTIDAE

Allomys (*Meniscomys*) *hippodus* Cope	American Museum
Allomys (*Meniscomys*) *liolophus* Cope	American Museum
Allomys (*Meniscomys*) *cavatus* Cope	American Museum
Allomys (*Meniscomys*) *nitens* Marsh, var. *multiplicatus* Cope	Yale University
Mylagaulodon angulatus Sinclair	University of California

CASTORIDAE

Steneofiber gradatus Cope	American Museum
Steneofiber peninsulatus Cope	American Museum

GEOMYIDAE

Pleurolicus sulcifrons Cope	American Museum
Pleurolicus leptophrys Cope	American Museum
Pleurolicus diplophysus Cope	American Museum
Entoptychus planifrons Cope	American Museum
Entoptychus cavifrons Cope	American Museum
Entoptychus minor Cope	American Museum
Entoptychus lambdoideus Cope	American Museum
Entoptychus crassiramis Cope	American Museum
Entoptychus rostratus Sinclair	University of California
Entoptychus sperryi Sinclair	University of California

MURIDAE

Peromyscus nematodon (Cope)[40]	American Museum
Peromyscus parvus Sinclair[40]	University of California

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[40] Primitive forms which might not be referred to existing genera if better known.

Paciculus lockingtonianus Cope	American Museum
Paciculus insolitus Cope	American Museum

LEPORIDAE

Lepus ennisianus Cope[40]	American Museum

PERISSODACTYLA

EQUIDAE

Mesohippus praestans (Cope)	American Museum
Mesohippus equiceps (Cope)	American Museum
Mesohippus brachylophus (Cope)	American Museum
Mesohippus longicristis (Cope)	American Museum
Mesohippus condoni Leidy	U. S. National Museum
Mesohippus anceps (Marsh)	Yale University
Mesohippus annectens (Marsh)	Yale University
Mesohippus acutidens Sinclair	University of California

LOPHIODONTIDAE

? Colodon (*Lophiodon*) *occidentalis* Leidy	U. S. National Museum

TAPIRIDAE

Protapirus robustus Sinclair	University of California

RHINOCEROTIDAE

Aceratherium pacificum Leidy	U. S. National Museum
Aceratherium hesperium Leidy	U. S. National Museum
Aceratherium truquianum Cope	American Museum
Aceratherium tubifer Cope	American Museum
Aceratherium annectens Marsh	Yale University
Diceratherium armatum Marsh	Yale University
Diceratherium nanum Marsh	Yale University

INDETERMINATE

Daeodon shoshonensis Cope	American Museum

CHALICOTHERIDAE

Moropus distans Marsh	Yale University
Moropus senex Marsh	Yale University

ARTIODACTYLA

ELOTHERIIDAE

Elotherium humerosum Cope	American Museum
Elotherium imperator Leidy	U. S. National Museum
Elotherium calkinsi Sinclair	University of California

SUIDAE

Thinohyus (*Bothrolabis*) *pristinus* Leidy	U. S. National Museum
Thinohyus (*Bothrolabis*) *trichaenus* Cope	American Museum
Thinohyus (*Bothrolabis*) *rostratus* Cope	American Museum
Thinohyus (*Bothrolabis*) *subaequans* Cope	Condon collection, University of Oregon
Thinohyus (*Bothrolabis*) *decedens* Cope	Condon collection, University of Oregon Supplementary type, University of California
Thinohyus (*Bothrolabis*) *lentus* Marsh	Yale University
Thinohyus (*Bothrolabis*) *socialis* Marsh	Yale University
Thinohyus (*Bothrolabis*) *osmonti* Sinclair	University of California

MERYCOIDODONTS

Agriochoerus trifrons Cope	American Museum
Agriochoerus guyotianus Cope	American Museum
Agriochoerus ryderanus Cope	American Museum
Agriochoerus ferox (Cope)	American Museum
Eporeodon occidentalis Marsh (*Eucrotaphus jacksoni* Leidy, part *Eucrotaphus major* Leidy, part)	Yale University
Eporeodon occidentalis leptacanthus (Cope)	American Museum
Eporeodon occidentalis pacificus (Cope)	American Museum
Eporeodon trigonocephalus (Cope)	American Museum
Eporeodon major longifrons (Cope)	American Museum
Eporeodon socialis Marsh	Yale University
Promerycochoerus superbus (Leidy) (*temporalis* Bettany)	U. S. National Museum
Promerycochoerus chelydra (Cope)	American Museum
Promerycochoerus macrostegus (Cope)	American Museum
Promerycochoerus leidyi (Bettany)	Sedgwickian Museum, Cambridge, England

CAMELIDAE

Miolabis (*Paratylopus*) *sternbergi* (Cope)	American Museum
Miolabis (*Paratylopus*) *cameloides* (Wortman)	American Museum

HYPERTRAGULIDAE

Hypertragulus calcaratus (?) Cope[41]	American Museum
Allomeryx planiceps Sinclair[42]	University of California

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[41] Not *calcaratus* but an undescribed species, Matthew, Bull. Am. Mus., Vol. 16, p. 316. *H. hesperius* of Hay's catalogue, Bull. 179, U. S. G. S., p. 675.

[42] The characters cited in the original description of this genus (Sinclair 1905) are, perhaps, insufficient to warrant separating it from *Hypertragulus*. It is retained for the present, pending a revision of the group.

TESTUDINATA

TESTUDINIDAE

Stylemys oregonensis Leidy (*S. nebrascensis* Cope)	Condon collection, University of Oregon

SQUAMATA

BOIDAE

Ogmophis oregonensis Cope	American Museum

The Fauna of the Lower Division.—The lower John Day has proved to be almost devoid of fossil remains, although careful search was made for them at a number of localities. The following forms are represented in the University of California's collections by fragmentary specimens too poor for specific determination:

Elotherium (large species).
Rhinoceros (genus and species indet.).

Mr. L. S. Davis remembers finding the skull of a Merycoidodont in the beds of this horizon some years ago, but definite information concerning it is not now obtainable.

The Fauna of the Middle Division.—The following list of species from the Diceratherium beds is based on material brought together by University of California parties collecting with the vertical distribution of species particularly in mind:

Temnocyon altigenis Cope.
Nothocyon latidens (Cope).
Nothocyon lemur (Cope).
Nothocyon geismarianus mollis Merriam, J. C.
Mesocyon coryphaeus (Cope).
Mesocyon josephi (?) (Cope).
Philotrox condoni Merriam, J. C.
Cynodictis (?) *oregonensis* Merriam, J. C.
Archaelurus debilis major Merriam, J. C.
Nimravus gomphodus Cope.
Allomys nitens Marsh.
Allomys hippodus (Cope).
Allomys cavatus (Cope).
Allomys liolophus (Cope).
Steneofiber peninsulatus Cope.
Steneofiber gradatus Cope.
Peromyscus nematodon (Cope).
Peromyscus parvus Sinclair.

Pleurolicus (?) sp.
Entoptychus planifrons Cope.
Entoptychus cavifrons Cope.
Entoptychus crassiramis Cope.
Entoptychus minor Cope.
Lepus ennisianus Cope.
Rhinoceros (genera and species not yet determined).
Mesohippus equiceps (Cope).
Elotherium sp.
Thinohyus (*Bothrolabis*) *osmonti* Sinclair.
Thinohyus (*Bothrolabis*) *decedens* Cope.
Thinohyus lentus (?) Marsh.
Agriochoerus guyotianus Cope.
Agriochoerus sp.
Eporeodon occidentalis Marsh.
Eporeodon occidentalis pacificus (Cope).
Atlomeryx planiceps Sinclair.
Hypertragulus sp.
Stylemys sp.

Owing to the characteristic color of the matrix of the Middle John Day it has been possible to expand the list of species peculiar to this horizon considerably by an examination of the type material in the Cope collection at the American Museum of Natural History. Judging from the color of the matrix, the following type specimens are probably from the Middle John Day:

Nothocyon geismarianus (Cope).
Nothocyon lemur (Cope).
Temnocyon altigenis Cope.
Mesocyon coryphaeus (Cope).
Archaelurus debilis Cope.
Nimravus gomphodus Cope.
Steneofiber peninsulatus Cope.
Steneofiber gradatus Cope.
Pleurolicus leptophrys Cope.
Entoptychus planifrons Cope.
Entoptychus minor Cope.
Entoptychus lambdoideus Cope.
Allomys hippodus (Cope).
Allomys cavatus (Cope).
Mesohippus equiceps (Cope).
Thinohyus (*Bothrolabis*) *pristinus* Cope.
Thinohyus (*Bothrolabis*) *rostratus* Cope.
Eporeodon occidentalis leptacanthus (Cope).

To these should be added *Pogonodon platycopis* Cope, the only known specimen of which was collected by Mr. L. S. Davis from the Middle John Day in Turtle Cove.

Combining both of these lists, the Middle John Day fauna, so far as known, contains the following forms:

Temnocyon altigenis Cope.
Nothocyon latidens (Cope).
Nothocyon lemur (Cope).
Nothocyon geismarianus (Cope).
Nothocyon geismarianus mollis Merriam, J. C.
Mesocyon coryphaeus (Cope).
Mesocyon josephi (?) (Cope).
Philotrox condoni Merriam, J. C.
Cynodictis (?) *oregonensis* Merriam, J C
Archaelurus debilis Cope.
Archaelurus debilis major Merriam, J. C.
Nimravus gomphodus Cope.
Pogonodon platycopis Cope.
Allomys nitens Marsh.
Allomys hippodus (Cope).
Allomys cavatus (Cope).
Allomys liolophus (Cope).
Steneofiber peninsulatus Cope.
Steneofiber gradatus Cope.
Peromyscus nematodon (Cope).
Peromyscus parvus Sinclair.
Pleurolicus (?) sp.
Pleurolicus leptophrys Cope.
Entoptychus planifrons Cope.
Entoptychus minor Cope.
Entoptychus cavifrons Cope.
Entoptychus crassiramis Cope.
Entoptychus lambdoideus Cope.
Lepus ennisianus Cope.
Rhinoceros, species indet.
Mesohippus equiceps (Cope).
Elotherium sp.
Thinohyus (*Bothrolabis*) *osmonti* Sinclair.
Thinohyus (*Bothrolabis*) *decedens* Cope.
Thinohyus (*Bothrolabis*) *pristinus* Cope.
Thinohyus (*Bothrolabis*) *rostratus* Cope.
Thinohyus lentus (?) Marsh.
Agriochoerus guyotianus Cope.
Agriochoerus sp.

Eporeodon occidentalis Marsh.
Eporeodon occidentalis pacificus (Cope).
Eporeodon occidentalis leptacanthus (Cope).
Allomeryx planiceps Sinclair.
Hypertragulus sp.
Stylemys sp.

The Middle John Day is characterized by abundant remains of *Eporeodon*, especially of the two smaller species *occidentalis* and *pacificus*, and by a great number of rodents, which have been obtained principally at two horizons, one at about the middle and the other at the top of the Diceratherium beds. Both horizons contain practically the same fauna. Next to *Eporeodon* in abundance the most common form is a *Hypertragulus*, fragmentary specimens of which occur at almost every exposure. Rhinoceros material is fairly abundant but usually fragmentary and possibly represents other genera in addition to *Diceratherium*. The smaller pigs of the genus *Thinohyus* are most common in the middle beds, but it can not yet be determined whether they are confined to this horizon.

The Fauna of the Upper Division.—The following are typical forms from the Upper John Day. The determinations are based on material in the University of California collection.

Nothocyon lemur (Cope).
Temnocyon altigenis Cope.
Mesocyon coryphaeus (Cope).
Mesocyon brachyops Merriam, J. C.
Pogonodon davisi Merriam, J. C.
Entoptychus planifrons Cope.
Entoptychus cavifrons Cope.
Entoptychus rostratus Sinclair.
Entoptychus sperryi Sinclair.
Lepus ennisianus Cope.
Rhinoceros (genera and species not yet determined).
Mesohippus equiceps (Cope).
Mesohippus acutidens Sinclair.
Protapirus robustus Sinclair.
Elotherium calkinsi Sinclair.
Elotherium sp.
Agriochoerus ferox (Cope).
Eporeodon sp.
Promerycochoerus superbus (Cope).

Promerycochoerus chelydra (?) (Cope).
Hypertragulus sp.
Stylemys sp.

The types of the following species not represented by material in the University of California collection are known with more or less certainty to have been found in the Upper John Day beds.

Temnocyon ferox Eyerman.[43]
Mesohippus praestans (Cope).[44]
Eporeodon trigonocephalus (Cope).[45]
Eporeodon major longifrons (Cope).[46]
Promerycochoerus macrostegus (Cope).[47]
Promerycochoerus leidyi (Bettany).[48]

The gravels and tuffs at the top of the Upper John Day which have been referred to on a preceding page as possibly constituting a separate faunal horizon have afforded the following forms:

Mylagaulodon angulatus Sinclair.
Protapirus sp.
Miolabis (*Paratylopus*) *cameloides* (Wortman).

The type of *Miolabis* (*Paratylopus*) *sternbergi* is stated by Wortman to be "from the lower beds of the John Day Valley." (= Diceratherium beds of Wortman). The matrix investing the skull is, however, quite unlike the Middle John Day tuffs, and resembles the uppermost part of the Upper John Day in which camel remains are particularly abundant. For the present it is omitted from the faunal list of either horizon.

Combining the various partial lists of Upper John Day species, the following forms may be regarded as characteristic of this division:

Nothocyon lemur (Cope).
Temnocyon altigenis Cope.
Temnocyon ferox Eyerman.

[43] Princeton University collection. Upper John Day, Turtle Cove. Communicated by Professor W. B. Scott.

[44] American Museum collection. Buff-colored matrix.

[45] American Museum collection. North Fork of the John Day River. The matrix is the characteristic buff-colored tuff of the upper division.

[46] Same locality as *E. trigonocephalus*.

[47] American Museum collection. Bridge Creek. The horizon is probably the Promerycochoerus beds.

[48] Bridge Creek. Probably from the Promerycochoerus beds.

Mesocyon coryphaeus (Cope).
Mesocyon brachyops Merriam, J. C.
Pogonodon davisi Merriam, J. C.
Entoptychus planifrons Cope.
Entoptychus cavifrons, Cope.
Entoptychus rostratus Sinclair.
Entoptychus sperryi Sinclair.
Lepus ennisianus Cope.
Mylagaulodon angulatus Sinclair.
Rhinoceros.
Mesohippus equiceps (Cope).
Mesohippus acutidens Sinclair.
Mesohippus praestans Cope).
Protapirus robustus Sinclair.
Protapirus sp.
Elotherium calkinsi Sinclair.
Elotherium sp.
Agriochoerus ferox (Cope).
Eporeodon sp.
Eporeodon trigonocephalus (Cope).
Eporeodon major longifrons (Cope).
Promerycochoerus superbus (Cope).
Promerycochoerus chelydra (Cope).
Promerycochoerus macrostegus (Cope).
Promerycochoerus leidyi (Bettany).
Hypertragulus sp.
Miolabis (*Paratylopus*) *cameloides* (Wortman).
Stylemys sp.

Promerycochoerus is the most common form in the Upper John Day, and is not known from the middle division. Its absence from the middle division affords an important means of discriminating the horizons in the field. Like *Promerycochoerus*, *Protapirus* is also unrepresented in the Middle John Day. The introduction of these two genera may be explained by their immigration from some other province, as they are without known ancestral forms in the Middle John Day. *Agriochoerus* decreases in abundance in the Upper John Day, where it is represented by bizarre forms like *A. ferox*. Large elotheres are more common than in the Diceratherium beds. The smaller hogs have not been found in the upper division. Rodents are not well represented. Camels have been found only in the uppermost beds of the series. Plains and forest types occur together in the same beds.

Age.—Stratigraphically, the John Day occupies a position between the Upper Clarno (Upper Eocene) and the Columbia Lava. From the latter it is separated by an interval of deformation, and sub-aerial erosion. Before considering the age of the John Day it will be advisable to present briefly what is known regarding the age of the lava.

The Columbia Lava is evidently referable to the earlier Miocene, as it is overlain by the Mascall of the later Miocene. Its correlative is the Yakima basalt of the Ellensberg quadrangle, which bears the same relation to the Ellensberg formation that the Columbia Lava does to the Mascall, the equivalent of the Ellensberg. By Smith[49] the age of the Yakima basalt is fixed as early or middle Miocene from the fact that the basalt rests unconformably on the Manastash formation (Upper Eocene = Clarno) without the intervention of the John Day.

The time equivalent of the unconformity at the top of the John Day can not be accurately measured. At a number of localities the upper beds are wanting, the lava resting on the Middle John Day. Elsewhere, the erosion is represented by gulches carved into the John Day tuffs and preserved beneath the lava cap. Taken in connection with the great thickness of the lava it seems reasonable to regard the volcanic and erosion intervals together as equivalent to a considerable part of the earlier Miocene.

A strict adherence to the three-fold subdivision of the Tertiary would necessitate placing the John Day in the Lower Miocene and the Columbia Lava in the Middle Miocene, since the former rests on the Upper Eocene and the latter is overlain by beds determined from their flora as Upper Miocene. Following the four-fold division which is becoming more and more generally accepted by American geologists, the John Day is referable mainly if not entirely to the Oligocene, and a study of its fauna has shown the propriety of such reference. "Taken together, the Canidae and Felidae of the John Day represent a stage of evolution somewhat more advanced than that reached in the White River and less advanced than that of the Loup Fork. Compared with the known faunas of Europe they appear to be not older than the Middle Oligocene of Fontainbleau and not as young as the Middle Miocene of Sansan."[50] It is not yet possible to speak so definitely regarding the degree of advancement of other phyla in the John Day fauna, but the persistence of primitive types (*Elotherium*, *Agriochoerus*, *Mesohippus*, *Protapirus*) and the entire absence of the hypsodont camels and horses characteristic of the Middle and Upper Miocene of North America is certainly striking, and, when combined with the stratigraphic evidence just presented, favors the reference of the John Day formation mainly to the Oligocene, although it does not exclude the possibility that the Upper John Day may overlap in part on the Lower Miocene, of which the fauna is at present incompletely known.[51]

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[49] G. O. Smith. Professional Paper U. S. G. S., No. 19, p. 16.

[50] Merriam, J. C. Univ. Cal. Publ. Geol., Vol. 5, p. 64.

As all the John Day species, so far as known at present, appear to be peculiar to the Oregon province, attempts at close correlation have failed. Owing to the lack of common species and the fact that it is often impossible to decide whether certain species are more advanced than others within the limits of the same genus, it is unsafe to base any attempt at very close correlation on the presence of common genera alone.

With the close of the John Day epoch, the total extinction of many genera and even families took place in Oregon. As examples may be cited *Mesohippus*, *Elotherium*, *Agriochoerus*, *Eporeodon*, *Protapirus*, the Carnivora, and many of the Rodentia. Not a single species survived. Just how the process of extinction operated in the region under discussion, whether by the dying out of long persistent stocks, or by emigration and by transformation in the ordinary processes of evolution is not fully apparent. This faunal break exceeds in importance all differences existing between the lesser subdivisions of the John Day series.

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[51] Peterson, O. A. The Agate Spring Fossil Quarry. Annals Carnegie Museum, Vol. 3, pp. 487–494, 1906. The Miocene Beds of Western Nebraska and Eastern Wyoming and their Vertebrate Fauna. Annals Carnegie Mus., Vol. 4, No. 1, March 21, 1907.

Matthew, W. D. A Lower Miocene Fauna from South Dakota. Bull. Am. Mus. Nat. Hist., Vol. 23, p. 169, March 14, 1907.

The recent papers of Peterson and Matthew, appearing since this article was prepared, have shown the existence on the eastern side of the Cordilleran range of early Miocene faunas closely related to that of the John Day. In both western Nebraska and South Dakota faunas are found containing generic types previously known only from the John Day; but in both of these regions the stage of evolution of the forms most closely related to John Day types, as also of the total assemblage of forms, seems a little more advanced than that of the John Day. As the eastern and western faunas were quite distant from each other geographically, and might therefore be expected to differ somewhat, it is not impossible that the earlier portion of the Miocene beds east of the Cordilleran range corresponds in time to the upper portion of the John Day. A more complete knowledge of all of these faunas will be necessary before their exact relationships can be determined, and most important in this connection is the study of scattered patches of middle Tertiary beds which are geographically intermediate.

The Mascall

Fauna.—In discussion the Mascall fauna, the possibility of mixture with the overlying Rattlesnake must generally be considered, since bones which have weathered out of the Rattlesnake gravels are frequently found resting on the Mascall, and as most of the material from the latter formation is detached from the matrix it is often very difficult to avoid confusing the two faunas.

A list of the species previously reported and probably derived from these beds is given below. Those marked with an asterisk may possibly be Rattlesnake.

Lutrictis lycopotamicus Cope.
Archaeohippus ultimus (Cope).
Parahippus brevidens (Marsh).
Protohippus medius Cope.
Protohippus avus Marsh.
Pliohippus spectans Cope.
Merychippus isonesus (Cope).
**Neohipparion occidentale* (Leidy).
**Neohipparion sinclairi* (Wortman).
Aceratherium oregonense (Marsh).
**Platygonus rex* Marsh.
Promerycochoerus obliquidens (Cope).
Merycochoerus sp.[52]
Miolabis transmontanus Cope.
Alticamelus altus (Marsh).
Palaeomeryx borealis (Cope).
Plioplarchus septemspinosus Cope.

A number of these forms are not represented in the University of California collection and further exploration will be necessary before the two faunas can be fully separated.

Remains of the following species were collected by the University parties at localities where there can be little doubt of their Mascall origin. A large amount of material is unfortunately too fragmentary to permit of specific determination. To this list there is added the type of *Tephrocyon rurestris* (Condon), which is known to be from the Mascall beds.

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* Possibly Rattlesnake.

[52] Matthew. Bull. Am. Mus., Vol. 12, p. 72.

Canis sp.
Tephrocyon rurestris (Condon).
Mylagaulus sp.[53]
Steneofiber sp.
Peromyscus (?) sp.
Lepus sp.
Mastodon sp.
Archaeohippus ultimus (Cope).
Archaeohippus, sp. indesc.
Parahippus brevidens (Marsh).
Neohipparion, sp. indet.
Pliohippus (?) sp.
Merychippus isonesus (Cope).
Merychippus relictus (Cope).
Rhinoceros, sp. and genus indet.
Camelid.[54]
Cervine (*Palaeomeryx?*) sp. *a*.
Cervine (*Palaeomeryx?*) sp. *b*.
Merycoidodont.[55]
Gravigrade edentate.
Clemmys saxea Hay.
Plioplarchus septemspinosus Cope.[56]

A comparison of the Mascall and John Day faunas brings out a number of important contrasts. With the exception of *Lepus* and *Peromyscus*,[57] few genera survived the interval of faunal migration and extinction at the close of the John Day, notably *Promerycochoerus*, *Miolabis* and *Steneofiber*. With the repopulation of the region, hypsodont horses and large camels adapted to existence on grassy plains appear. With these are associated proboscideans and deer of which no ancestral forms are known in the John Day. Evidently a large proportion of the Mascall fauna came into Oregon after the basalt floods had ceased, migrating from other provinces, where its evolution took place during the time of extravasation of the lava or in even earlier time.

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[53] Collected by Mr. L. S. Davis for Professor K. A. von Zittel from the Mascall near Dayville. A part of the maxilla supporting P^4.

[54] Astragali and calcanea. Size of *Alticamelus altus*.

[55] The presence of a small Merycoidodont is indicated by a mandibular fragment with the greater part of the milk dentition from the Mascall near Dayville. A caniniform premolar was obtained from the Mascall beds on the divide between Camp Creek and Crooked River.

[56] From the leaf-bearing beds of the lower part of the Mascall near the old Van Horn ranch. A single species from this locality.

[57] See foot-note 40 on p. 552.

Age.—Knowlton has referred the Mascall to the Upper Miocene, basing this conclusion on the affinities and relationships of the forty or more species of plants confined to this formation, but he remarks that if dependence were placed on the distribution of those species which are not confined to the Mascall, "the tendency would be to regard them as not younger than Lower Miocene, or even possibly as old as the Upper Eocene."[58] The Mascall has been correlated by him with the Ellensberg formation.[59] A previous correlation with the auriferous gravels of California is no longer retained.[60]

The Mascall fauna has attained about the same stage of evolution as the faunas of the Pawnee Creek and Deep River horizons of Colorado and Montana, respectively. *Merychippus isonesus* is common to all three,[61] while *Parahippus brevidens* (*Desmatippus crenidens* Scott) is common to the Deep River and Mascall. This evidence is deemed sufficient for approximate correlation of the three sets of beds. Both faunal and stratigraphic evidence favors the reference of the Mascall to the middle or later portion of the Miocene.

THE RATTLESNAKE

The type specimens of the following species are supposed to have been derived from the Rattlesnake beds:

Neohipparion occidentale (Leidy).[62]
Neohipparion sinclairi (Wortman).[62]
Platygonus rex Marsh.[63]

To these should be added, from specimens in the University of California collection, *Pliohippus supremus* (Leidy), some indeterminate rhinoceros material, a large hog, a camel of the size of

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[58] Knowlton. Fossil Flora of the John Day Basin. Bull. 204, U. S. G. S., p. 108.

[59] Ellensberg quadrangle, U. S. G. S. Atlas. Note in text.

[60] Bulletin 204, U. S. G. S., pp. 107–108.

[61] Listed by Matthew from the Deep River. Memoirs Amer. Mus., Vol. 1, p. 374.

[62] "From the loose gravels overlying the Cottonwood beds." Matthew. Bull. Am. Mus., Vol. 12, p. 70. This reference was based on Wortman's recollection of his collections made twenty years previous to the publication of Matthew's list. Communicated by Dr. Matthew.

[63] Mr. L. S. Davis remembers collecting what he believes to be the type specimen of this species from the Rattlesnake gravels.

Alticamelus altus, fragmentary remains of a smaller camel, and portions of the carapace and plastron of a tortoise (*Clemmys hesperia* Hay).

The known fauna of the Rattlesnake is too scanty to afford a good basis for age determination or to serve satisfactorily for purposes of correlation. It is evidently pre-Pleistocene, and as the Rattlesnake is separated from the Mascall by a considerable interval of erosion its age may be fixed with some degree of probability as Pliocene.

LIST OF CONTRIBUTIONS TO THE GEOLOGY AND PALAEONTOLOGY OF THE JOHN DAY REGION

Bettany, G. T.

1876—On the Genus Merycochoerus (Family Oreodontidae), with Descriptions of two New Species. Q. J. G. S., Vol. 32, pp. 259–273.

Blake, W. P.

1867—Locality of Secondary Fossils in Oregon. Amer. Jour. Sc., Vol. 44, p. 118.

Calkins, F. C.

1902—A contribution to the Petrography of the John Day Basin. Univ. of Cal. Publications. Bull. Dept. Geol., Vol. 3, pp. 109–172.

Condon, Thomas.

1871—The Rocks of the John Day Valley. Overland Monthly, May, 1871, p. 393.

1902—The Two Islands and What Came of Them. Portland, Oregon.

Cope, E. D.

1878—On Some of the Characters of the Miocene Fauna of Oregon. Pal. Bulletin, No. 30, pp. 1–16, Dec. 3d, 1878; Proc. Am. Phil. Soc., Vol. 18, pp. 63–78.

1879—On the Extinct Species of Rhinoceridae of North America and Their Allies. Bull. U. S. Geol. and Geog. Surv. Tys., Vol. 5, pp. 227–237; Am. Nat., Vol. 13, pp. 771a–771j.

1879—Observations on the Faunae of the Miocene Tertiaries of Oregon. Bull. U. S. G. S. of the Terrs., Vol. 5, article 3.

1879—Second Contribution to a Knowledge of the Miocene Fauna of Oregon. Pal. Bulletin, No. 31, pp. 1–7. Dec., 1879. Proc. Am. Phil. Soc., Vol. 18, pp. 370–376; Jan., 1880.

1879—Additions to the List of Miocene Vertebrata of Oregon. Am. Nat., Vol. 13, pp. 131, 132.

1879—On the Genera of Felidae and Canidae. Proc. Acad. Nat. Sci., Phila., Vol. 31, pp. 168–194.

1879—American Aceratheria. Am. Nat., Vol. 13, p. 333.

1879—Description of Archaelurus debilis and Hoplophoneus platycopis. Amer. Nat., Vol. 13, p. 798a.

Cope, E. D.—*Continued.*

1879—A new Anchitherium. Am. Nat., Vol. 13, pp. 462–463.

1880—Corrections of the Geological Maps of Oregon. Am. Nat., Vol. 14, pp. 457–458.

1880—On certain Tertiary Strata of the Great Basin. Proc. Am. Phil. Soc., Vol. 19, p. 61.

1880—Notes on Sabre-tooths. Am. Nat., Vol. 14, p. 143.

1880—Miocene Fauna of Oregon (abstract). Am. Nat., Vol. 14, p. 58.

1880—A new Hippidium. Am. Nat., Vol. 14, p. 223.

1880—On the Extinct Cats of North America. Am. Nat., Vol. 14, pp. 833–858.

1881—On the Nimravidae and Canidae of the Miocene Period. Bull. U. S. Geol. and Geog. Survey of the Terrs., Vol. 6, article 3, pp. 165–181.

1881—Miocene Dogs. Am. Nat., Vol. 15, p. 497.

1881—Review of the Rodentia of the Miocene Period of North America. Bull. U. S. Geol. and Geog. Survey of the Terrs., Vol. 6, article 15, pp. 361–386.

1881—The Rodentia of the American Miocene. Am. Nat., Vol. 15, pp. 586–587.

1882—The Tertiary Formations of the Central Region of the United States. Am. Nat., Vol. 16, pp. 177–195.

1883—The Extinct Rodentia of North America. Pts. I–III, Am. Nat., Vol. 17, pp. 43–57, 165–174, 370–381.

1883—On the Extinct Dogs of North America. Am. Nat., Vol. 17, pp. 235–249.

1884—Synopsis of the Species of Oreondontidae. Proc. Am. Phil. Soc., Vol. 21, pp. 503–572.

1884—The History of the Oreodontidae. Am. Nat., Vol. 18, pp. 280–282.

1884—The Vertebrata of the Tertiary Formations of the West, Book I, Rept. U. S. Geol. Survey of the Terrs. (Hayden), Vol. 3.

1886—On two new species of three-toed horse from the Upper Miocene, with note on the fauna of the Ticholeptus beds. Proc. Am. Phil. Soc., Vol. 23, pp. 357–361.

1886—The Phylogeny of the Camelidae. Am. Nat., Vol. 20, pp. 611–624.

1886—The Vertebrate Fauna of the Ticholeptus Beds. Am. Nat., Vol. 20, pp. 367–369.

1887—The Perissodactyla. Am. Nat., Vol. 21, pp. 985–1007, 1060–1076.

1888—On the Dicotylinae of the John Day Miocene. Proc. Am. Phil. Soc., Vol. 25, pp. 62–79.

1889—A Review of the North American Species of Hippotherium. Proc. Am. Phil. Soc., Vol. 26, pp. 429–458.

1888—The Artiodactyla. Am. Nat., Vol. 22, pp. 1079–1095.

1889—The Artiodactyla. Am. Nat., Vol. 23, pp. 111–136.

1889—On a species of Plioplarchus from Oregon. Am. Nat., Vol. 25, 625–626.

Dall, W. H.

1898—A Table of the North American Tertiary Horizons, Correlated with One Another and with Those of Western Europe, with Additions. Eighteenth Ann. Rept. U. S. G. S. Pt. II.

Eyerman, John.

1894—Preliminary notice of a new species of Temnocyon, and a new genus from the John Day Miocene of Oregon. Am. Geologist, Vol. 14, pp. 320–321.

1896—The genus Temnocyon and a new species thereof, and the new genus Hypotemnodon, from the John Day Miocene of Oregon. Am. Geol., Vol. 17, pp. 267–287.

Gidley, J. W.

1906—A New Genus of Horses from the Mascall Beds, with Notes on a Small Collection of Equine Teeth in the University of California. Bull. Am. Mus., Vol. 22, pp. 385–388.

Hatcher, J. B.

1902—Origin of the Oligocene and Miocene Deposits of the Great Plains Proc. Am. Phil. Soc., Vol. 41, pp. 113–131. (Correlation table, p. 118.)

Hay, O. P.

1903—Two New Species of Fossil Turtles from Oregon. Univ. of Cal. Publications. Bull. Dept. Geol., Vol. 3, pp. 237–241.

Hyatt, A.

1894—Trias and Jura in the Western States. Bull. Geol. Soc. Amer., Vol. 5, pp. 401, 418–420.

King, Clarence.

1878—U. S. Geological Exploration of the Fortieth Parallel. Vol. 1, pp. 413, 423, 458.

Knowlton, F. H.

1902—Fossil Flora of the John Day Basin, Oregon. U. S. Geol. Survey Bulletin, No. 204.

Ellensberg Quadrangle. U. S. G. S. Note in text correlating Ellensberg and Mascall beds.

Le Conte, Joseph.

1874—On the Great Lava Flood of the West, and on the Structure and Age of the Cascade Mountains. Am. Jour. Sci. (3), Vol. 7, pp. 167–180, 259–267.

Leidy, Joseph.

1870—(Remarks on a collection of fossils from Dalles City, Oregon). Proc. Acad. Nat. Sci., Phila., Vol. 22, pp. 111–113.

1871—Remarks on fossils from Oregon. Proc. Acad. Nat. Sci., Phila., Vol. 23, pp. 247–248.

1873—Contributions to the Extinct Vertebrate Fauna of the Western Territories. Rept. of the U. S. Geol. Survey of the Terrs. (Hayden), Vol. 1.

Lesquereux, Leo.

1878—Fossil Plants of the Auriferous Gravel Deposits of the Sierra Nevada. Memoirs Mus. Comp. Zool., Vol. 6, No. 2. (Certain Mascall plant species included, through insufficient labeling, with those from the Auriferous Gravels of California.)

1883—Cretaceous and Tertiary Floras. U. S. Geol. Survey of the Terrs., Vol. 8, pp. 239–255.

1889—Recent Determinations of Fossil Plants from Kentucky, Louisiana, Oregon, California, Alaska, etc., with Descriptions of New Species. Proc. U. S. Nat. Mus., 1888, Vol. 11, pp. 11–38.

Marsh, O. C.

1873—Notice of New Tertiary Mammals. Am. Jour. Sci. (3), Vol. 5, pp. 407–410, 485–488.

1874—Notice of New Equine Mammals from the Tertiary Formation. Am. Jour. Sci. (3), Vol. 7, pp. 247–258.

1875—Ancient Lake Basins of the Rocky Mountain Region. Am. Jour. Sci. (3), Vol. 9, pp. 49–52.

1875—Notice of New Tertiary Mammals. Am. Jour. Sci. (3), Vol. 9, pp. 239–250.

1877—Notice of some new Vertebrate fossils. Am. Jour. Sci. (3), Vol. 14, pp. 249–256.

1885—The Gigantic Mammals of the Order Dinocerata. 5th Ann. Rept. U. S. G. S., pp. 243–302. (Figures *Eporeodon socialis*, figs. 128, 129.)

1894—Description of Tertiary Artiodactyles. Am. Jour. Sci. (3), Vol. 48, pp. 259–274.

1895—The Reptilia of the Baptanodon Beds. Am. Jour. Sci., Vol. 50, p. 405.

Matthew, W. D.

1899—A Provisional Classification of the Fresh-water Tertiary of the West. Bull. Am. Mus. Nat. Hist., Vol. 12, pp. 19–75.

1907—A Lower Miocene Fauna from South Dakota. Bull. Am. Mus., Vol. 23, pp. 169–219.

Merriam, J. C.

1900—Classification of the John Day beds. (Abstract.) Science, n. s., Vol. 11, pp. 219–220.

1900 and 1901—Geological Section through the John Day Basin (abstract). Bulletin Geol. Soc. Am., Vol. 12; Jour. Geol., Vol. 9, pp. 71–72.

1901—A Contribution to the Geology of the John Day Basin. Bulletin Dept. of Geology Univ. of Cal., Vol. 2, pp. 269–314.

1901—The John Day Fossil Beds. Harper's Monthly Magazine, Vol. 102, pp. 581–590, March.

1906—Carnivora from the Tertiary Formations of the John Day Region. Univ. Calif. Pub. Geology, Vol. 5, No. 1, Nov. 30.

Merriam, J. C. and W. J. Sinclair.

1903—The Correlation of the John Day and the Mascall (abstract). Jour. Geol., Vol. 11, pp. 95–96.

Newberry, J. S.

1883—Brief Description of Fossil Plants, Chiefly Tertiary, from Western North America. Proc. U. S. Nat. Mus., Vol. 5, pp. 502–513.

1898—The Later Extinct Floras of North America. Monograph 35, U. S. Geological Survey.

Osborn, H. F.

1900—The Geological and Faunal Relations of Europe and America During the Tertiary Period and the Theory of the Successive Invasions of an African Fauna. Science, N. S., Vol. 11, pp. 561–574. (Correlation of John Day with European horizons.)

1900—Correlation between Tertiary Mammal Horizons of Europe and America, with Third Trial Sheet. Annals N. Y. Acad. Sci., Vol. 13, pp. 1–72. (Correlation of John Day with European horizons.)

1907—Tertiary Mammal Horizons of North America. Bull. Am. Mus., Vol. 23, pp. 237–253.

Russell, I. C.

1897—A Reconnaissance in Southeastern Washington. U. S. G. S. Water Supply and Irrigation Papers, No. 4. (Correlates John Day with Ellensberg formation.)

1905—Preliminary Report on the Geology and Water Resources of Central Oregon. U. S. Geol. Survey, Bull. No. 252, p. 58.

1903—Notes on the Geology of southwestern Idaho and southeastern Oregon. U. S. Geol. Surv., Bull. No. 217.

Scott, W. B.

1890—Beiträge zur Kentniss der Oreodontidae. Morpholog. Jahrb., Vol. 16, pp. 319–395.

1893—The Mammalia of the Deep River Beds. Trans. Am. Phil. Soc., Vol. 17, p. 60. (Discusses Cope's correlation of the Mascall and Deep River beds.)

1893—On a New Musteline from the John Day Miocene. Am. Nat., Vol. 27, p. 658.

1895—On the Tertiary Lacustrine Formations of North America. Rept. Brit. Assn. for the Adv. of Sci., p. 681.

1899—The Selenodont Artiodactyla of the Unita Eocene. Trans. Wagner Free Inst. Science., Phila., Vol. 6, pp. ix–xiii, 1–121. (Figures *Hypertragulus calcaratus* so-called.)

Sinclair, W. J.

1901—The Discovery of a New Fossil Tapir in Oregon. Jour. Geol., Vol. 9, pp. 702–707.

1903—Mylagaulodon, A New Rodent from the Upper John Day of Oregon. Am. Jour. Sci., Vol. 15, pp. 143–144.

1905—New or Imperfectly Known Rodents and Ungulates from the John Day Series. Bull. Dept. Geol., Univ. of Cal., Vol. 4, pp. 125–143.

1906—Some Edentate-like Remains from the Mascall Beds of Oregon. Univ. Calif. Pub. Geology, Vol. 5, No. 2.

Smith, G. O.

1903—Contributions to the Geology of Washington. Professional Paper No. 19, U. S. G. S. (Correlation of Manastash formation with Upper Clarno.)

Stearns, R. E. C.

1900—Fossil Land Shells of the John Day Region, with Notes on Related Living Species. Wash. Acad. Sci. Proc., Vol. 2, pp. 651–658.

1902—Fossil Shells of the John Day Region. Science N. S., Vol. 15, pp. 153–154; also Ibid. p. 393.

1906—Fossil Shells from the John Day and Mascall Beds of Oregon. Univ. Calif. Pub. Geology, Vol. 5, No. 3.

Sternberg, Charles H.

1881—The Miocene beds of the John Day River, Oregon. Kansas City Review, Vol. 4, pp. 730–733.

Washburne, C.

1903—Notes on the Marine Sediments of Eastern Oregon. Jour. Geol., Vol. 11, p. 224.

White, C. A.

1885—On Marine Eocene Fresh-water Miocene and other Fossil Mollusca from Western North America. Bulletin U. S. G. S., No. 18.

Whitney, J. D.

1867—Notice of the Occurrence of Silurian Series in Nevada. Proc. Cal. Acad. Nat. Sci., Vol. 3, p. 309, Jan.

Wortman, J. L.

1898—The Extinct Camelidae of North America and some Associated Forms. Bull. Am. Mus., Vol. 10, pp. 93–142.

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Issued October 12, 1907

AN AMERICAN PLIOCENE BEAR

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INTRODUCTION

ALTHOUGH the bear group is well known in some of the latest Cenozoic faunas of the Western Hemisphere, the one or two occurrences of very fragmentary material reported to represent this family in American deposits older than Pleistocene have been considered doubtful. In the Old World, members of the Ursidae are found in formations ranging from Miocene to Recent, and in view of available evidence it is assumed generally that the New World bears are comparatively recent immigrants, the earliest arrivals having come from Asia to North America near the beginning of Pleistocene time.

The North American Pleistocene bears comprise two groups; the *Ursus* type, represented by forms closely related to existing species of this continent; and the peculiar short-faced arctotheres, having no living representatives in North America, but closely related to the spectacle bear of South America. In the Pleistocene of South America *Arctotherium* is known by several species, but *Ursus* is not represented. There is then apparent basis for the theory that *Arctotherium* arrived in North America in advance of bears of the *Ursus* type and reached South America before *Ursus* crossed from the Old World. If this view expresses the history of migration of bears in America, remains of *Arctotherium*, or of a type ancestral to this genus, might be expected in earliest Pleistocene or Pliocene deposits of North America. The absence of

By John C. Merriam, Chester Stock, and Clarence L. Moody. *University of California Publications, Bulletin of the Department of Geology*, vol. 10, no. 7, pp. 87–109, November 1, 1916.

Arctotherium and of well authenticated remains of near relatives of this division of the bear group from North American deposits older than those containing *Ursus* has sometimes been interpreted to indicate the migration of *Arctotherium*, or of its ancestors, to South America by some route other than that through North America.

In the course of a special study of the later Tertiary deposits of eastern Oregon carried on by the Department of Palaeontology of the University of California in the summer of 1916, remains of a member of the bear group were discovered by Chester Stock and Clarence L. Moody in beds of the Rattlesnake Pliocene of the John Day region. The significance of this discovery, especially with relation to other studies on correlation and migration of Tertiary mammal faunas, makes desirable a statement of the evidence in advance of a full report on the Rattlesnake fauna.

Occurrence

Remains of the Pliocene bear (no. 22362) were found in the Rattlesnake formation exposed on the East Fork of the John Day River in northeastern Oregon. The locality is situated near the center of N.W. $\frac{1}{4}$ sec. 30, T. 12 S., R. 26 E., Willamette Base Line and Meridian, Grant County, Oregon, approximately five and one-half miles west of Dayville, and not over three-fourths of a mile south of the type section of the Rattlesnake formation. The specimen was found on a low ridge between Rattlesnake Creek and Little Rattlesnake Creek.

In the typical area the Rattlesnake formation is tilted at an angle of approximately five degrees and rests upon a basement formed by sharply deformed, truncated strata of the Mascall Middle Miocene. The present canyon of the John Day River cuts through the basin of accumulation of the Rattlesnake. In the bottom of this canyon Pleistocene mammal remains are found in terrace deposits laid down after the canyon had attained approximately its present form. The stage of the Rattlesnake is thus limited on one side by antecedent Middle Miocene and by the period of deformation and extensive erosion intervening between deposition of the Mascall and beginning accumulation of the Rattlesnake. On the other side this stage is limited by the date of subsequent Pleistocene terraces and the period of canyon cutting intervening between the close of the Rattlesnake and beginning accumulation of the terrace deposits.

The known mammalian fauna of the Rattlesnake comprises between twenty and thirty species. The available representation will be fully discussed in an early publication. The horses are presumably the most important elements of the fauna for purposes of palaeontologic and geologic correlation. The Equidae are represented by species of the *Hipparion* and *Pliohippus* groups having their nearest relatives in beds referred to the early Pliocene of the Great Basin and Pacific Coast provinces. The view that the Rattlesnake fauna is related to that of the Thousand Creek Pliocene in Nevada receives support through the discovery of a horn-core of the peculiar antelope *Sphenophalos* in the Rattlesnake, in the course of the past season's work. This antelope has heretofore been known only from the Thousand Creek, where it occurs in association with twisted-horn antelopes of the *Ilingoceros* type.

In the locality at which the bear remains were found the Rattlesnake formation consists principally of a series of cross-bedded gravels alternating with varicolored tuffs and sands. A persistent rhyolite flow occurs at a high horizon in the formation. Pebbles in any single stratum are usually of comparable dimensions, but sharp changes occur in passing from one bed to another. Thus a stratum with bowlders attaining a diameter of one foot may immediately overlie a bed in which the largest pebbles have a diameter of not more than one-half inch. It was in a layer of the finer gravel that the bear remains were discovered. The bed seems to be lenticular, but this appearance may be due to occurrence of the gravels on the summit of a ridge. Mascall Miocene is exposed in the bed of Rattlesnake Creek to the north of the ridge upon which the gravels were found. This ridge has an approximate elevation of 150 feet above the level of the stream, thus placing the horizon at which the bear remains occurred well up in the Rattlesnake section. The erosion of Rattlesnake and Little Rattlesnake creeks has removed a large part of the formation south of the course of the former stream, and the section is known to be thicker toward the south. It has therefore not been found possible to ascertain the exact distance below the summit of the section represented by the bed in which the bear specimen was found. This horizon is believed to be stratigraphically within the limits of about 100 feet below the top of the rhyolite cap which forms the summit of the section at the type locality of the Rattlesnake.

The material representing the Pliocene bear includes the most important parts of the dentition, with six or seven representative elements of the limbs. There is good reason for considering that all of these specimens are derived from one individual. The preservation of the bones and teeth corresponds in general to that of other mammal remains obtained in the type section of the Rattlesnake formation.

Dentition

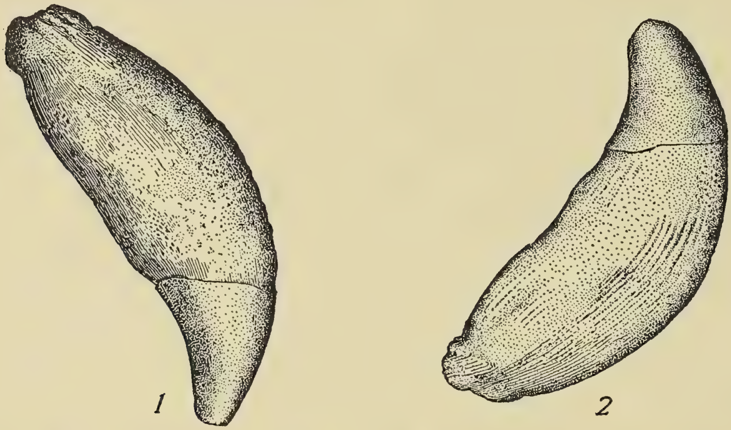
The dentition of specimen no. 22362 from the Rattlesnake Pliocene includes practically all essential elements. From the upper jaws there are represented I$\underline{2}$, I$\underline{3}$, C, P$\underline{1}$, P$\underline{4}$, and M$\underline{2}$. The first upper molar is the only superior tooth of importance lacking. From the mandible only the canines and M$\overline{2}$ were found. While it is to be regretted that the lower carnassial is not available, it should be noted that the forms most nearly related to this particular type show less variation in M$\overline{1}$ than in P$\underline{4}$, M$\underline{2}$, and M$\overline{2}$, all of which are at hand. The teeth present illustrate so fully the characters of the dentition as a whole that it is possible to make those comparative studies most important in determination of the relationships of this animal.

The two upper *incisors* present are much worn. So far as can be determined, they are of approximately the type seen in *Arctotherium*, but are larger than the corresponding elements in *A. simum* of the California Pleistocene.

The large, heavy-fanged *canines* (figs. 1 and 2) are of the characteristic ursid type. The crowns of the upper canines have dimensions and proportions near those of *A. simum* of Potter Creek Cave. The roots may be larger relative to the size of the crown in the Rattlesnake specimen, but are not thicker in either transverse or anteroposterior diameter. In the lower canines, as in *A. simum*, the crowns are sharply concave on the posterior side. As in the upper canines, the crowns are near the size of those in *A. simum*, but the roots seem relatively large.

P$\underline{1}$ shows a form closely approaching that in the corresponding tooth of *A. simum*. This tooth (fig. 3) has a simple single root; and the crown consists of a single cusp, which extends to the anterior and posterior borders of the tooth in a well-marked longitudinal ridge or crest. The anterior ridge is noticeably convex on the outer side, and drops off abruptly or may be concave on the median side. A distinctly marked ridge of the cingulum on the antero-internal side unites anteriorly with the principal crest.

Fortunately both the right and left *upper carnassials* ($\mathrm{P}\underline{4}$) are represented. These teeth (figs. 4*a* to 4*c*) are large and unusually well developed for members of the Ursidae. They differ markedly from all specimens of *Ursus* and *Arctotherium* known to the writers, and approach closely the type of $\mathrm{P}\underline{4}$ known in the several species of *Hyaenarctos* (figs. 5 to 7). In the Oregon species the protocone is slightly larger than the tritocone. The deuterocone is very large, approximating in its cross-section the size of the protocone; and is situated so far forward that its anterior border is not posterior to



Figs. 1 and 2. *Indarctos(?) oregonensis*, n. sp. Canine teeth, no. 22362, lateral view, × ½. Fig. 1, upper canine; fig. 2, lower canine. Rattlesnake formation, John Day Valley, Oregon.

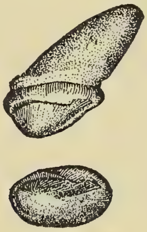
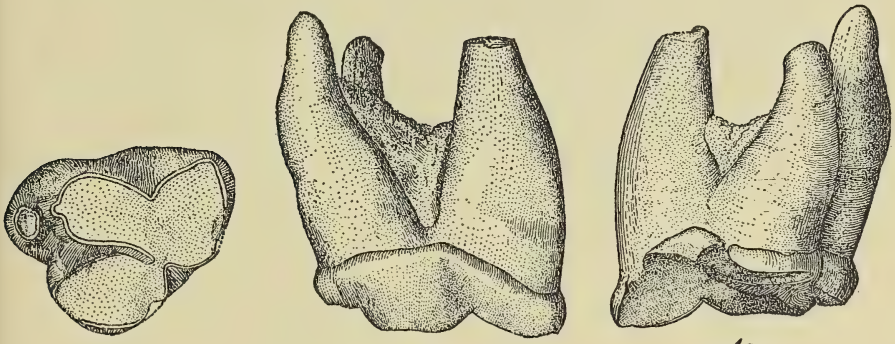


Fig. 3. *Indarctos(?) oregonensis*, n. sp. $\mathrm{P}\underline{1}$, no. 22362, inner and occlusal views, natural size. Rattlesnake formation, John Day Valley, Oregon.

the corresponding border of the protocone as in *Ursus* and *Arctotherium.* A large protostyle is present. The tooth is distinctly three-rooted, a large and widely divergent root supporting the deuterocone. The outer contour of the tooth shows a distinct concavity of the cingulum opposite the posterior side of the protocone.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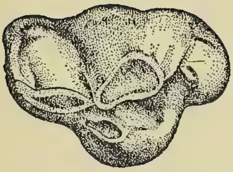
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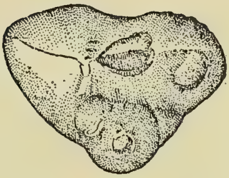
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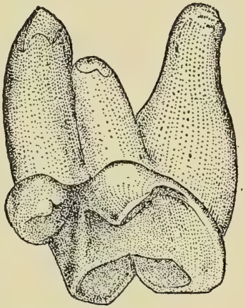
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FIGS. 4*a* TO 4*c*. *Indarctos*(?) *oregonensis*, n. sp. P$\underline{4}$, no. 22362, natural size. Fig. 4*a*, occlusal view; fig. 4*b*, outer view; fig. 4*c*, inner view. Rattlesnake formation, John Day Valley, Oregon.

FIG. 5. *Hyaenarctos insignis* P. Gervais. P$\underline{4}$, occlusal view, natural size. Montpellier, France. (After Gervais.)

FIG. 6. *Hyaenarctos palaeindicus* Lydekker. P$\underline{4}$, occlusal view, natural size. Siwalik beds, India. (After Lydekker.)

FIG. 7. *Hyaenarctos insignis* P. Gervais. P$\underline{4}$, inner view, natural size. Montpellier, France. (After Gervais.)

P$\underline{4}$ differs from the corresponding tooth of *Arctotherium* in the relatively large size of the deuterocone; in the support of the deuterocone upon a distinct, widely diverging inner or third root; in the situation of the deuterocone as far forward as the protocone;

and in the presence of a large, distinctly separated protostyle. In all of the characters in which this tooth differs from *Arctotherium* it resembles *Hyaenarctos*. If isolated from other material, P4 would certainly be considered as representing *Hyaenarctos* rather than the *Arctotherium* type.

The upper carnassial of no. 22362 may be more primitive than that of *Arctotherium* in the anterior position of the deuterocone, and is more specialized in the presence of a large protostyle. In the Oregon form the anterior border of the deuterocone is situated approximately as far forward as the anterior border of the protocone, and in *Hyaenarctos* the deuterocone tends to take the same position. In *Arctotherium*, and in bears of the *Ursus* type, the deuterocone is shifted far back and away from what is considered a normal position of this tubercle in the modern Carnivora, and is commonly situated opposite the notch between protocone and tritocone. The protostyle, which is so largely developed in the Oregon specimen and in *Hyaenarctos*, may be suggested in some arctothere specimens, and is figured by Blainville[1] in his illustration of the dentition of *Tremarctos ornatus*, the Recent South American relative of the arctotheres. It is therefore possible that a protostyle was at one time present on P4 of *Arctotherium*.

The *posterior upper molars* (M2) (figs. 8*a* to 9) of the bear from the Rattlesnake beds most nearly resemble those of the ursid type described by Pilgrim[2] from the middle or upper Siwalik beds of India under the name of *Indarctos salmontanus* (fig. 12). M2 of specimen 22362 resembles the type of *I. salmontanus* in its unusual relation of width to anteroposterior diameter, and in the stage of development of the heel. The anteroposterior and transverse diameters are almost identical with those of the type of *I. salmontanus*. The heel is a trifle longer in the Oregon specimen, but tends to be slightly wider in the Indian form. The difference in width of heel is possibly due in some part to difference in stage of wear in the specimens compared. As in *I. salmontanus*, the paracone and metacone of no. 22362 are clearly defined, the paracone being considerably larger than the metacone. In *I. salmontanus* the antero-internal region of the tooth consists of a large ridge divided into two tubercles of which the anterior is the larger. In the Oregon specimen the heavy antero-internal ridge is present, but the teeth are too much worn to show distinctly whether this area was divided into two elements. On the left tooth such a separation is suggested. In no. 22362, as in *I. salmontanus*, there is evidence of a large tubercle immediately behind the antero-internal ridge, corresponding evidently to the hypocone. This tubercle appears somewhat larger in Pilgrim's figure of *I. salmontanus* than it is in the left tooth of no. 22362. On the right tooth the hypocone may have been somewhat larger. The extreme posterior end of the heel consists of a transverse ridge which is largely worn down.

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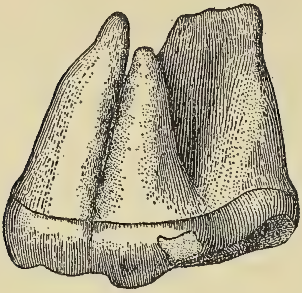
[1] Blainville, H. M. D., Osteographie des mammifères, Atlas 2, pl. 12, 1864.

[2] Pilgrim, Guy E., Records, Geological Survey of India, vol. 44, part 3, pp. 225–233, pl. 20, 1914.

The proportions of the various areas of the tooth in no. 22362 are near those of the type of *Indarctos*. The anteroposterior diameter of the paracone is slightly less than it measures on Pilgrim's figure of *I. salmontanus*. The distance from the posterior end of the paracone to the posterior end of the tooth is slightly greater in no. 22362, as is also the distance from the middle of the metacone to the posterior end of the tooth. The distance from the middle of the metacone to the anterior end of the tooth is greater in *I. salmontanus*.

Considering that in no. 22362 $M\underline{2}$ is considerably worn, and allowing for individual variation, the resemblances between the Oregon specimen and the type of *I. salmontanus* are close. Small differences, such as the more distinctly circular cross-section of the metacone, the smaller hypocone, slightly longer heel, and wider trigon region in the Oregon form, suggest specific distinction such as would be expected in individuals so widely separated geographically.

The characters of $M\underline{2}$ in the Oregon form, and in *Indarctos salmontanus*, approach those of *Hyaenarctos* excepting in relative elongation of the heel. The two outer cusps of $M\underline{2}$ in *Hyaenarctos* may show somewhat stronger lateral compression than is noted in the Oregon form. The antero-internal ridge in *Hyaenarctos* may apparently show almost no separation into two divisions, or may be very distinctly divided as in *H. palaeindicus*, in which the hypocone region is imperfectly developed. In *H. punjabiensis* (fig. 11) an incipient heel is clearly shown, though it is much less pronounced than in *Indarctos*. As has been suggested by Pilgrim, an intermediate stage between the form seen in *H. punjabiensis* and that



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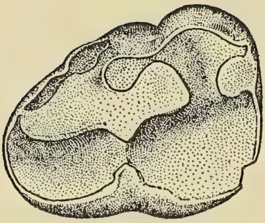

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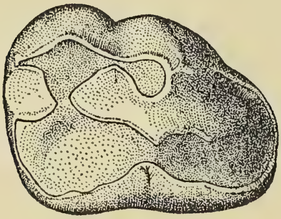

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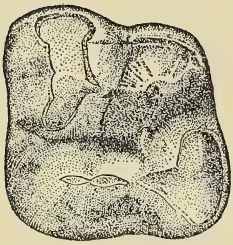

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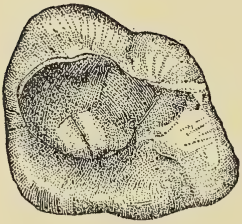

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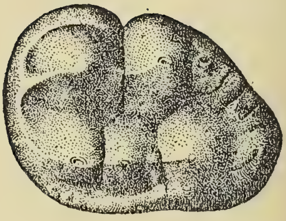

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Figs. 8*a* to 9. *Indarctos*(?) *oregonensis*, n. sp. M$\underline{2}$ of right and left sides, no. 22362, natural size. Fig. 8*a*, M$\underline{2}$ of left side, outer view; fig. 8*b*, M$\underline{2}$ of left side, occlusal view; fig. 9, M$\underline{2}$ of right side, occlusal view. Rattlesnake formation, John Day Valley, Oregon.

Fig. 10. *Hyaenarctos sivalensis* Falc. and Caut. M$\underline{2}$, occlusal view, natural size. Siwalik beds, India. (After Lydekker.)

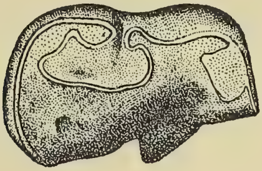
Fig. 11. *Hyaenarctos punjabiensis* Lydekker. M$\underline{2}$, occlusal view, natural size. Siwalik beds, India. (After Lydekker.)

Fig. 12. *Indarctos salmontanus* Pilgrim. M$\underline{2}$ of type specimen, occlusal view, natural size. Siwalik beds, India. (After Pilgrim.)

in the type of *I. salmontanus* might connect the two groups so closely that generic separation would be difficult if not impossible.

$\mathrm{M}\underline{2}$ of the Rattlesnake specimen is distinguished from that of *Arctotherium* by its greater width and much shorter talon. In *Arctotherium* the primitive quadritubercular portion of the tooth is longer anteroposteriorly and the heel is much longer. The arrangement of the tubercles is much the same in the two types, but the tubercles show stronger lateral compression in *Arctotherium*.

The arrangement of the roots supporting $\mathrm{M}\underline{2}$ in the Oregon specimen differs somewhat from that in *Arctotherium simum*. In no. 22362 (fig. 8*a*) there are two distinct external roots supporting the paracone and metacone regions. These roots in both available teeth are distinct, but are not widely separated. The inner and posterior regions of these teeth are supported by a large, broad root evidently composed of two parts, one of which supports the protocone region and the other originates above the hypocone and the region behind it.



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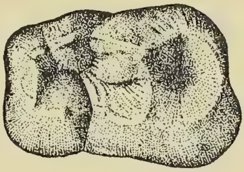

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FIG. 13. *Indarctos(?) oregonensis*, n. sp. $\mathrm{M}\bar{2}$, no. 22362, occlusal view, natural size. Rattlesnake formation, John Day Valley, Oregon.

FIG. 14. *Hyaenarctos punjabiensis?* Lydekker. $\mathrm{M}\bar{2}$, occlusal view, natural size. Siwalik beds, India. (After Lydekker.)

In *Arctotherium* there are also evidently four original root elements, but the roots beneath the paracone and metacone tend to diverge widely, the element above the metacone being in some cases united with the posterior root supporting the heel. In *Arctotherium* the root supporting the protocone may or may not unite with the root above the heel. In the type of *Indarctos salmontanus* the roots are not exposed.

$\mathrm{M}\bar{2}$, the only representative of the lower cheek-tooth dentition, is unfortunately so much worn that it illustrates comparatively few characters of the tuberculation (fig. 13). It is distinguished from the corresponding element in the dentition of *Hyaenarctos* and of certain forms of *Arctotherium* by the relative proportions of the trigonid and talonid regions. In the Oregon specimen the anteroposterior diameters of trigonid and talonid are, as nearly as can be determined, approximately equal. In *Hyaenarctos*, as is indicated by the measurements below, the talonid may have an anteroposterior diameter near one-half that of the trigonid. In *Arctotherium simum* the functional talonid may be longer than the trigonid. In some of the South American arctotheres, as in *Pararctotherium enectum* Ameghino, the proportions are as in *A. simum;* in others, as in *A. wingei* Ameghino, the talonid is relatively short. The increase in length of the heel region in *A. simum* is evidently related to the increase in area of $M\underline{2}$, as the talonid of $M\overline{2}$ articulates with the trigonid portion of $M\underline{2}$.

The tuberculation of $M\overline{2}$ represents only the inner side of the tooth, on which is shown the relatively high region occupied by the metaconid, and the lower more or less basin-like talonid region. The talonid possessed a rather wide hypoconid ridge, and two smaller cusps on the inner border as in *Hyaenarctos*.

The crown of $M\overline{2}$ is supported upon two roots of which the posterior is the larger.

Measurements of Dentition

	No. 22362
C, upper, anteroposterior diameter at base of enamel	*a*29.8 mm.
C, upper, transverse diameter at base of enamel	20.0
C, upper, length of root, measured along posterior border	76.7
C, lower, anteroposterior diameter at base of enamel	30.0
C, lower, transverse diameter at base of enamel	*a*21.3
C, lower, length of root, measured along posterior border	73.8
$P\underline{1}$, anteroposterior diameter	12.4
$P\underline{1}$, transverse diameter	7.1

	No. 22362 Left side	No. 22362 Right side	Indarctos salmontanus
$P\underline{4}$, anteroposterior diameter measured along outer side	31.7 mm.	31.0	
$P\underline{4}$, width across deuterocone	22.6	*a*20.9	
$P\underline{4}$, anteroposterior diameter of protocone at base	14.1	13.9	
$P\underline{4}$, anteroposterior diameter of protostyle	4.7	4.6	
$M\underline{2}$, greatest anteroposterior diameter	35.3	35.2	35 (35.5*)
$M\underline{2}$, anterior end of tooth to posterior end of paracone	13.8	14.0	14.8*
$M\underline{2}$, posterior end of paracone to posterior end of tooth	21.5	21.2	20.9*

Measurements of Dentition—*Continued*

	No. 22362 Left side	No. 22362 Right side	Indarctos salmontanus
M$\underline{2}$, anterior end of tooth to middle of metacone..	17.8 mm.	17.5	19.8*
M$\underline{2}$, middle of metacone to posterior end of tooth..	17.5	17.6	15.7*
M$\underline{2}$, width of tooth across paracone.............	26.8	27.2	27.0*
M$\underline{2}$, width of tooth across metacone.............	24.6	24.0	25.2*
M$\underline{2}$, anterior side of hypocone to posterior end of tooth......................................	17.6	15.6	15.4*
Length of M$\underline{2}$ compared with width of M$\underline{2}$......	1.31%	1.29%	1.29%

	No. 22362	A. simum No. 3004	Hyaenarctos punjabiensis?	Hyaenarctos? palaeindicus
M$\bar{2}$, anteroposterior diameter...........	32.0 mm.	30.4	30.5	30.0
M$\bar{2}$, anteroposterior diameter of trigonid..	15.8	14.9	19.0	16.5
M$\bar{2}$, anteroposterior diameter of functional talonid region..................	16.2	15.5	11.5	13.5
M$\bar{2}$, transverse diameter across talonid...	*a*21.3	18.4	19.3	19.2

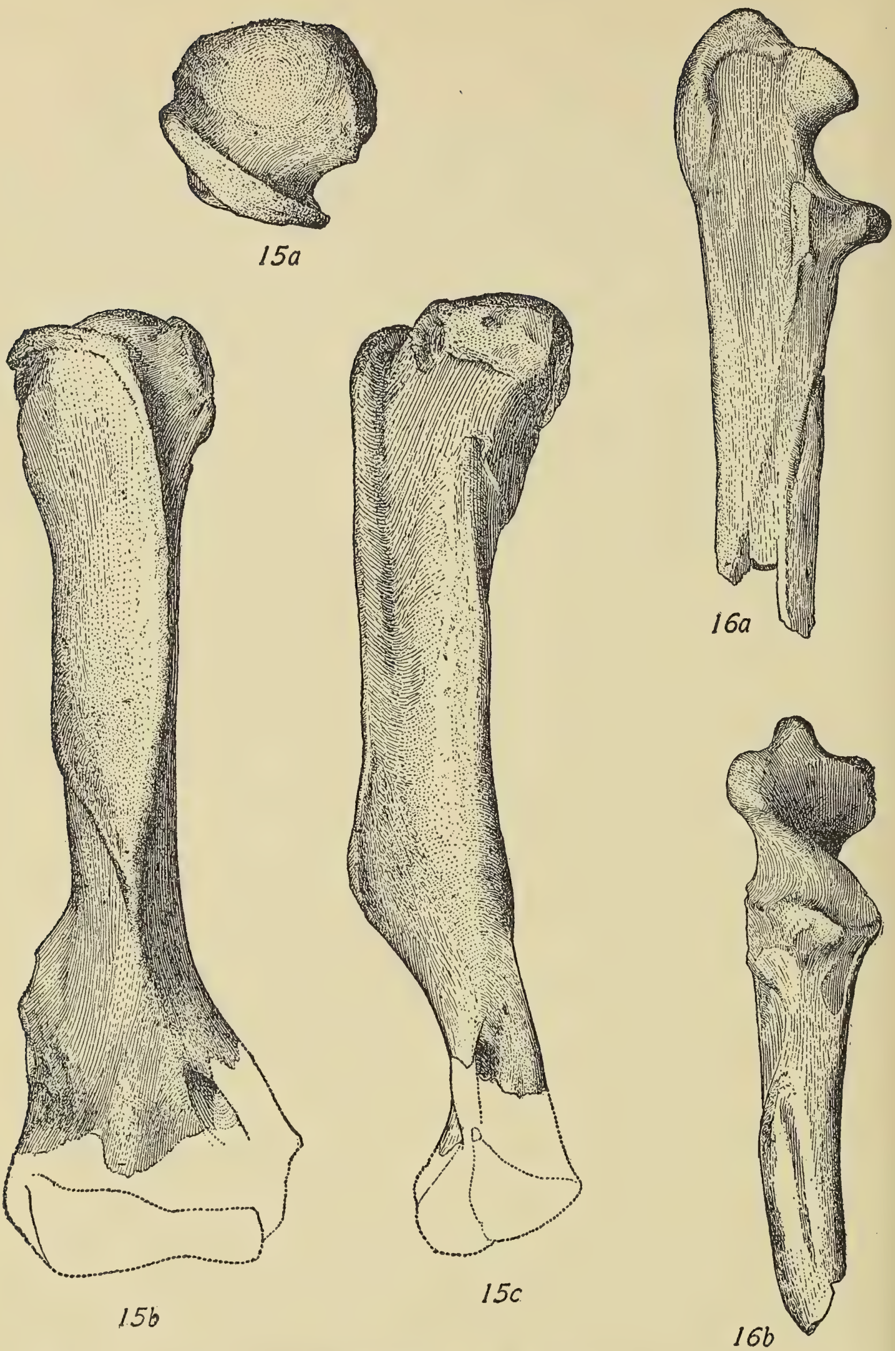
a, approximate.

* Measurements taken on Pilgrim's figure of M$\underline{2}$.

Skeletal Elements

The skeleton of no. 22362 is represented by the greater part of the humerus, half of the ulna, a fifth metacarpal, the navicular and cuboid, a second metatarsal, and several phalanges.

The right *humerus*, the first element of the Pliocene bear to be discovered, is nearly complete. A portion of the distal end had rotted away, and a small part of the proximal end is missing. This element (figs. 15*a* to 15*c*) is slightly longer and considerably more massive than that of specimens of *Arctotherium simum* from Potter Creek Cave and from Rancho La Brea. This difference between the Oregon form and the California Pleistocene *Arctotherium* is well shown in transverse diameter and thickness of the narrowest portion of the shaft at the lower end of the pectoral ridge. The supinator ridge is strongly developed as in *A. simum*, and is higher or wider than in either the Potter Creek Cave or the Rancho La Brea specimens. The flat area between the deltoid and pectoral ridges is more strongly marked and wider than in the California *Arctotherium* specimens. The lower end of this area also extends relatively much nearer the distal end of the shaft than in *A. simum*, and in side view (fig. 15*c*) is seen to project farther anteriorly.



Figs. 15*a* to 16*b*. *Indarctos*(?) *oregonensis*, n. sp. Humerus and ulna, no. 22362, × ¼. Fig. 15*a*, humerus, proximal view; fig. 15*b*, humerus, anterior view; fig. 15*c*, humerus, inner view. Fig. 16*a*, ulna, outer view; fig. 16*b*, ulna, anterior view. Rattlesnake formation, John Day Valley, Oregon.

A large entepicondylar foramen is present as in *Arctotherium.* The bar of bone forming the outer boundary of this foramen is largely broken away, but the remaining portion appears relatively heavier than in *Arctotherium.* The upper end of the foramen seems more broadly rounded than the superiorly narrowed foramen in *A. simum.*

On the whole the humerus is of a much more massive type than that of the California *Arctotherium*, and in this respect suggests the relatively heavy skeletal elements of *Hyaenarctos.*

The proximal half of the right *ulna* (figs. 16*a* and 16*b*) resembles in many respects the corresponding element of *Arctotherium simum*, but it is much larger and more massive than the California Pleistocene specimens. The anteroposterior diameter or greater width of the shaft seems relatively longer in no. 22362 than in the *Arctotherium* of California, and one might assume that in the Pliocene form this element was relatively somewhat stronger and heavier. The olecranon region of no. 22362 is longer than in *A. simum* and the anterior tuberosity of the olecranon is considerably higher. The posterior region of the olecranon is sharply twisted toward the inner side as in *Ursus* and *Arctotherium.* The anterior tuberosity is separated from the twisted posterior angle of the olecranon by a sharply marked concave surface which is not represented on the olecranon in *Arctotherium* and *Ursus.* The greater sigmoid cavity is deep and the lesser sigmoid cavity is distinctly concave.

In no. 22362 the ulna differs from a specimen described as *Hyaenarctos* from the Siwaliks of the Saharanpur district by Lydekker.[3] The Indian specimen was assumed by Lydekker to represent *Hyaenarctos*, although not found with other material representing that genus. It shows a somewhat longer olecranon, and a much more prominent anterior tuberosity than appears in the Oregon specimen. The anterior tuberosity is also nearer the proximal border of the greater sigmoid cavity in the Indian form. Lydekker called attention to the similarity of the Indian specimen to the ulna of *Amphicyon.*

Metacarpal 5 (figs. 17*a* to 17*d*) resembles in general the form of this element in the bears, especially that in *Arctotherium.* The Oregon specimen differs greatly in proportions from *A. simum* and *A. californicum* of the California Pleistocene. In no. 22362 this element has almost exactly the same length as specimen 3040 representing *A. simum* from Potter Creek Cave, but is very much thicker and heavier than the Potter Creek Cave specimen. The thickness of no. 22362 approximates that in the type of *A. californicum* from the Pleistocene of Rancho La Brea, but the shaft in the Rancho La Brea specimen is much longer and more slender. The Oregon specimen differs from the known California arctotheres in details of structure of metacarpal 5 as well as in proportions. In no. 22362 the distal articulation is more strongly bulbous on the superior side, and the median inferior keel is thicker and decidedly more prominent at the posterior end. At the distal end of the superior surface of the shaft there is a marked depression immediately posterior to the bulbous distal articulation, whereas in the California arctotheres this area may be flat rather than concave as in no. 22362. Also at the distal end of the inferior surface of the shaft there is a distinct concavity in the Oregon specimen, while in *A. simum* and *A. californicum* this region tends to be convex. In the middle of the superior surface of the shaft no. 22362 is strongly convex along the anteroposterior contour, while in the California *Arctotherium* specimens this outline is nearly straight. The proximal articular face of no. 22362 is narrower transversely than in either *A. simum* or *A. californicum*.

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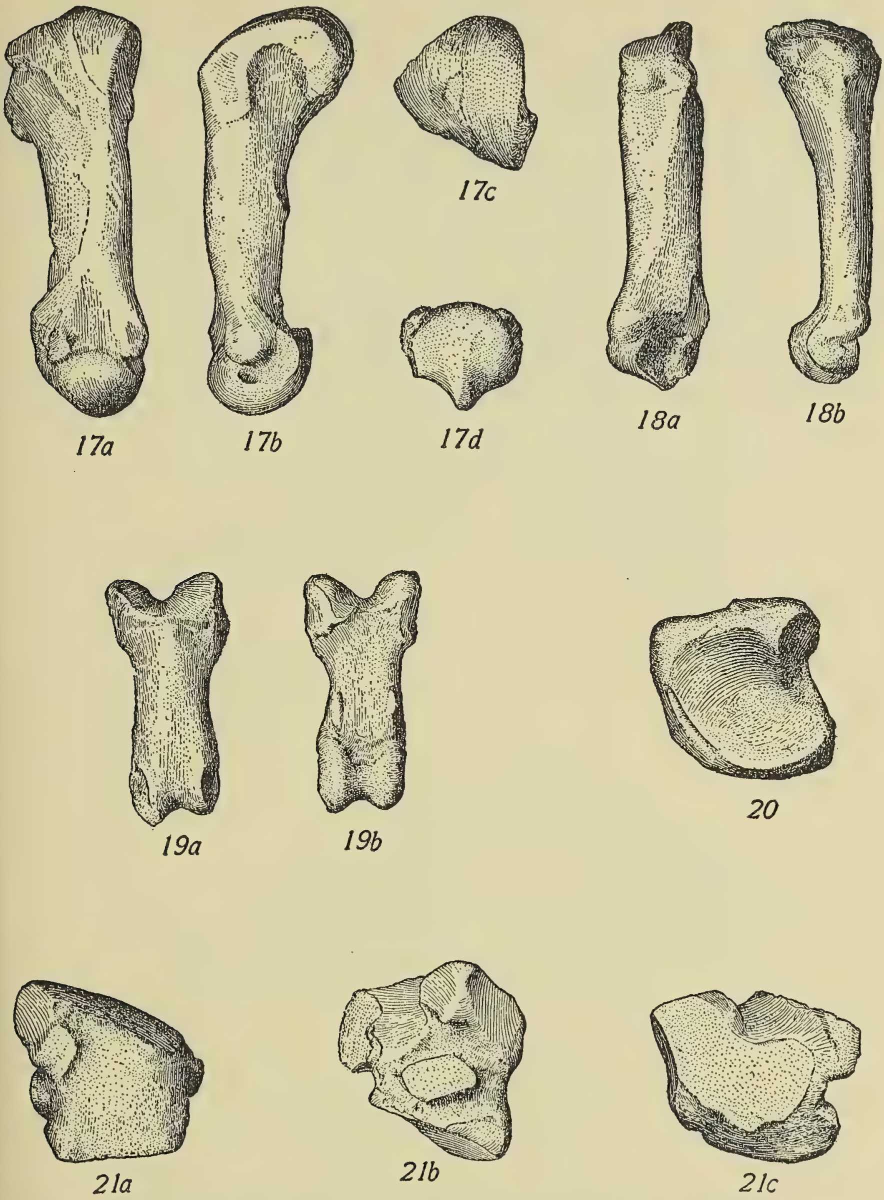
[3] Lydekker, R., Records, Geol. Survey of India, vol. 21, part 4, p. 145, 1888.

The specimen representing *metatarsal 2* (figs. 18*a* and 18*b*) is not as well preserved as the fifth metacarpal, and less satisfactory material of *Arctotherium* is available for comparison. In this metapodial, as in metacarpal 5, the tendency is toward somewhat greater thickness than in *Arctotherium*, but the element does not appear relatively as short compared with the corresponding element of *Arctotherium* as is the case in metacarpal 5. At the distal end the keel is somewhat more prominent than that in a specimen of *A. simum* from Potter Creek Cave.

A *navicular* (fig. 20) of the left foot is somewhat larger than the corresponding bone in the specimen of *A. simum* from Potter Creek Cave. The differences in the form of the element are not large. Although the navicular in no. 22362 is noticeably broader than the corresponding tarsal element in *Arctotherium* from Potter Creek Cave, it has approximately the same depth. In the Pliocene specimen the facet for the astragalus is not as deeply concave as



Figs 17*a* to 21*c*. *Indarctos*(?) *oregonensis*, n. sp. No. 22362, × ½. Fig. 17*a*, metacarpal 5, dorsal view; fig. 17*b*, metacarpal 5, median view; fig. 17*c*, metacarpal 5, proximal view; fig. 17*d*, metacarpal 5, distal view. Fig. 18*a*, metatarsal 2, dorsal view; fig. 18*b*, metatarsal 2, inner view. Fig. 19*a*, phalanx 1, dorsal view; fig. 19*b*, phalanx 1, ventral view. Fig. 20, navicular, proximal view. Fig. 21*a*, cuboid, dorsal view; fig. 21*b*, cuboid, median view; fig. 21*c*, cuboid, proximal view. Rattlesnake formation, John Day Valley, Oregon.

that in *Arctotherium.* The ventral portion of the articulating surface for the cuboid is larger and truncates the lateral margin more acutely than in the latter genus. Along the external border of the navicular this surface is less extensive than in *Ursus.* The union of the median and ventral borders is less distinctly rounded than in *A. simum.* The distal articulating surface is obscurely divided for the cuneiform elements. The ventral tubercle is large.

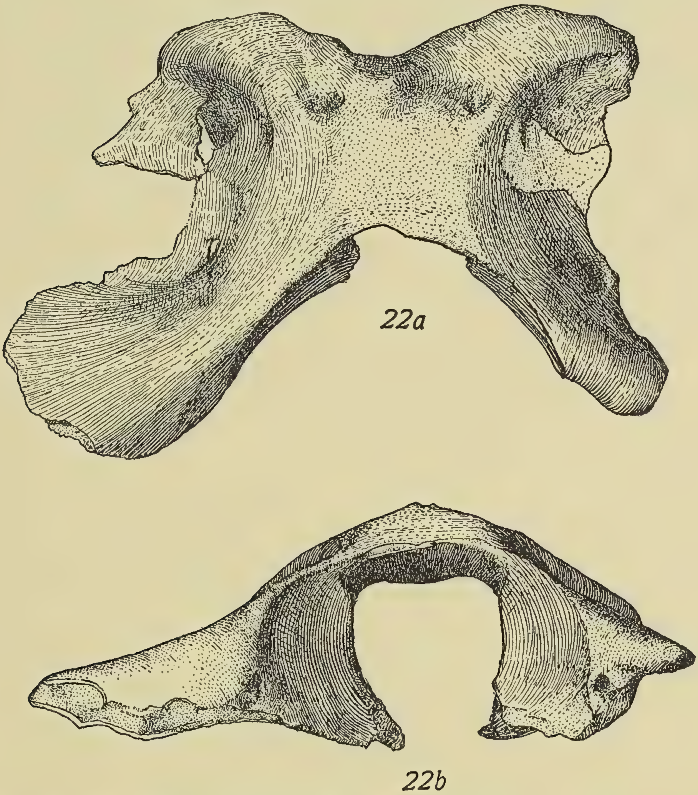
The *cuboid* (figs. 21*a* to 21*c*) possesses a long inner side and approaches more nearly a cuboidal form than does the corresponding element in the Recent *Ursus.* The cuboid of the Pleistocene *Arctotherium* from Potter Creek Cave is in this regard intermediate between that of no. 22362 and *Ursus.* In contrast to *Arctotherium* the angle between the dorsal plane and the plane of the metatarsal facet in the Pliocene cuboid is less acute.

The larger cuboid facet for the navicular is subtriangular. It is separated from an inner facet for the astragalus by a right angle, and is directed decidedly toward the ventral side. In *Arctotherium* and in *Ursus* this surface is directed more toward the inner side of the cuboid and is separated from the astragalar facet by an obtuse angle. The distal end of the boundary between the navicular and astragalar facets is truncated by a very small articulating surface also for the navicular. The latter has a greater dorso-ventral extent in *Arctotherium.*

The concave cuboid facet for the astragalus differs in its greater size and rectangular form from that in *Arctotherium* and in the Recent *Ursus.* Distal to this facet and widely separated from it is a large and flat articulating surface for the external cuneiform. In *A. simum* this surface is broadly confluent with the navicular facet. It is situated farther to the ventral side in no. 22362 than in the cuboid of *A. simum.* Only a single facet articulates with the external cuneiform at the distal margin of the cuboid.

The metatarsal facet of the cuboid is triangular and relatively smaller than in *Arctotherium.* On the ventral side of the cuboid the transverse ridge is situated farther proximally, especially toward the outer end, and the inner end is not as thick as in *Arctotherium.* The peroneal groove is much deeper than in either *Arctotherium* or *Ursus,* indicating a well developed peroneal muscle.

Two *phalanges* of the proximal series were recovered. One of the specimens (figs. 19*a* and 19*b*) is much longer than the other. They are both much larger than the first phalanges in *Ursus* and *Arctotherium simum* under observation. Both are noticeably compressed dorso-ventrally, as in the bears. The distal end is flexed downward, giving a distinct longitudinal arch to the dorsal surface. The proximal extremity is relatively broad and its ventral border is deeply notched.



Figs. 22*a* and 22*b*. Atlas associated with type specimen of *Indarctos* (?) *oregonensis*. No. 22362?, × ½. Fig. 22*a*, dorsal view; fig. 22*b*, posterior view. Rattlesnake formation, John Day Valley, Oregon.

An *atlas* (figs. 22*a* and 22*b*) found associated with rib fragments near the locality of no. 22362 represents a very large carnivore with characters differing from those of *Arctotherium*, the true bears, and such other carnivores as would be expected to occur in this formation. The atlas is much larger than that of an *Arctotherium* specimen from Potter Creek Cave, and differs from it structurally in several particulars. The lateral wings are broken, but seem to have been broad and to have extended with a wide sweep posteriorly somewhat as in *Ursus*. The posterior portion of the lateral wings extends behind the facets for articulation with the axis, as in *Smilodon*, without an interruption or notch such as appears in *Arctotherium*, *Ursus*, the dogs, and the true cats. In the specimen found near no. 22362 the extension of the wings behind the axis facets is buttressed by a high superior ridge which runs across the region in which the notch would be situated in the true bears or in *Arctotherium*. In this particular this atlas is again similar to that of *Smilodon*. One of the most important characters is found in the position of the vertebrarterial foramen, which in the Pliocene specimen is situated low down at the posterior border of the lateral wings, and immediately behind the facets for the axis. This situation is much as in *Smilodon*. In *Ursus* the posterior opening of this foramen is situated high up on the posterior side of the lateral wings. In *Arctotherium* it is situated considerably in advance of the postero-superior border of the wings. The position of this foramen in *Arctotherium* resembles more closely that of the dogs than in the case of *Ursus*.

The atlas from the Rattlesnake differs from that of the cats and the dogs in that the passage for the vertebral artery through the anterior side of the lateral wings is in an enclosed foramen instead of in a groove or notch in the anterior border. In this respect this atlas resembles that of *Ursus* and *Arctotherium*.

The characters of the atlas found near no. 22362 resemble those of the bears in the nature of the anterior portion of the vertebrarterial passage, resemble the cats in the nature of the posterior extremity of this canal, and resemble *Smilodon* in the form of the posterior border of the lateral wings. It is interesting to note that, whereas the atlas of *Arctotherium* is in certain respects more dog-like than that of *Ursus*, the Rattlesnake specimen differs widely from the dogs in the particular characters in which *Arctotherium* approaches them, and in these characters the Rattlesnake form resembles *Smilodon* more closely.

MEASUREMENTS OF SKELETAL PARTS

Humerus—	No. 22362
Length from head to radial articulating surface	*a*490 mm.
Anteroposterior diameter of head	*a*122

Measurements of Skeletal Parts—*Continued*

	No. 22362
Transverse diameter of head at tuberosities	*a*108.3 mm.
Anteroposterior diameter of shaft at distal end of deltoid crest	81.4
Least transverse diameter of shaft	53.6
Width of distal end	*a*158
Ulna—	
Distance from proximal end of greater sigmoid cavity to end of olecranon	80.3
Greatest anteroposterior diameter at coronoid	98.6
Greatest transverse diameter of shaft distal to greater sigmoid cavity	38.4
Metacarpal 5—	
Greatest length	103.6
Greatest anteroposterior diameter of proximal end	39
Transverse diameter of proximal end	*a*32.4
Transverse diameter at middle of shaft	21.5
Transverse diameter of distal end	*a*30
Metatarsal 2—	
Greatest length	94
Anteroposterior diameter of proximal end	*a*28.2
Transverse diameter of proximal end	*a*18.3
Transverse diameter at middle of shaft	18
Anteroposterior diameter at middle of shaft	12.8
Navicular—	
Greatest width	44.2
Greatest depth	46
Cuboid—	
Greatest proximo-distal diameter	40.4
Greatest transverse width	*a*49.4
Depth of metatarsal facet	36.8
Width of metatarsal facet	34.2
Phalanx 1—	
Greatest length	61.2
Width of proximal end	28.8

a, approximate.

RELATIONSHIPS

Although the representation of dentition and skeleton of the Oregon Pliocene bear is scanty, the elements available for study are fortunately among the most important that could be selected for comparative study. In the dentition the second upper molar and the upper carnassial have larger significance than all other members of the dental series for the particular comparison before us.

The broader relationships of the Rattlesnake bear are as clearly shown by $M\underline{2}$ and $P\underline{4}$ as they could be by $M\overline{1}$, while the greater variability of these two upper teeth tells the story with more detail and gives expression to the closer affinities. The few skeletal elements present, though leaving much to be desired, show characters of high value in estimating the more intimate relationships of this form.

The Oregon Pliocene bear approximates the characters of *Indarctos salmontanus* Pilgrim in the structure of M2, the only available tooth representing that genus. The characters seen in the type of *Indarctos* and in the Oregon specimen are not found in other known forms. These characters are most nearly approached in M2 of *Hyaenarctos*, *Arctotherium*, and *Aeluropus;* and are intermediate between those of *Hyaenarctos* and *Arctotherium.* In the characters of P4 the Oregon specimen does not differ essentially from the several known species of *Hyaenarctos*, but is distinctly different from *Arctotherium*, *Aeluropus*, and all other known forms referred to the bear group.

If as is indicated by the characters of M2 the Oregon form belongs to the same general group of bears as *Indarctos salmontanus*, and shows approximately the same stage of evolution, it seems probable that the Siwalik *Indarctos* also possessed the *Hyaenarctos* type of P4. From slender evidence furnished by strength of the maxilla and form of a small portion of the posterior border of the alveolus of P4, Pilgrim[4] inferred that P4 of *I. salmontanus* was large and possessed a distinct inner root; and that its inner cusp or deuterocone did not occupy an extreme posterior position as in *Helarctos*, in all modern bears, and in the Pliocene and Pleistocene types referable to *Ursus.* With such evidence as is at hand it may be assumed that P4 of Pilgrim's *Indarctos* was not materially different from that in the Oregon specimen.

The characters of the massive limb elements of the Oregon specimen, so far as they are known, suggest the limb type of *Hyaenarctos*, and indicate a rather wide separation from *Arctotherium.*

The sum of the known characters of the Oregon bear, specimen 22362, represent a type near *Hyaenarctos*, but tending toward *Arctotherium* in the development of its last upper molar. The Oregon form cannot be sharply separated from the Siwalik type of *Indarctos* on the basis of available material. Differences in proportions of the tubercles of M2 suggest the specific divergence which is to be expected in forms found in regions so widely separated geographically as India and Oregon. The Oregon form may be referred tentatively to the genus *Indarctos* with the specific name *oregonensis*.

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[4] Pilgrim, G. E., Records, Geol. Surv. India, vol. 44, part 3, p. 230, 1914.

The *Indarctos* group is nearer to *Hyaenarctos* than to *Arctotherium*, and as suggested by Pilgrim[5] the discovery of a type inter mediate between *Hyaenarctos punjabiensis* and *Indarctos salmontanus* might make it difficult to establish a generic separation between *Indarctos* and *Hyaenarctos*.

The occurrence in the Oregon Pliocene of a form closely allied to an Indian Siwalik type suggests close faunal relationship of Asia and North America in early Pliocene time. The presence of a form of the *Hyaenarctos* type with characters tending toward those of *Arctotherium* in the North American Pliocene also gives support to the assumption that the American *Arctotherium* is derived from a line passing near that of *Hyaenarctos*. It is now possible to consider the origin of *Arctotherium* in America rather than in Eurasia. As no bears of the *Ursus* type are known from the Pliocene of America, we may conceive of *Arctotherium* as originating in North America in the Pliocene and entering South America before *Ursus* was present in the New World. This would account for the large Pleistocene development of *Arctotherium* in South America in absence of *Ursus*, though the two groups appear together in the North American Pleistocene.

A large lower carnassial of a bear-like animal (figs. 23*a* and 23*b*) from the brown coal of Tehuichila near the boundary between the states of Hidalgo and Vera Cruz, Mexico, was thought by Freudenberg[6] to resemble *Hyaenarctos*. This specimen was found in beds containing a *Hipparion* fauna, and presumed to be of upper Miocene or lower Pliocene age. An excellent cast of the Mexican specimen kindly furnished by Dr. Freudenberg is available for comparative study. This tooth resembles in many respects the lower carnassial of a specimen referred to *Hyaenarctos punjabiensis* by Lydekker.[7] The general form of both the trigonid and talonid portions of the tooth is like that of *Hyaenarctos*, and the proportions compared in anteroposterior diameter are approximately the same. Unfortunately the Mexican specimen is broken in the region of the metaconid, but as nearly as can be determined this portion of the tooth may not have been widely different from that of the Indian genus.

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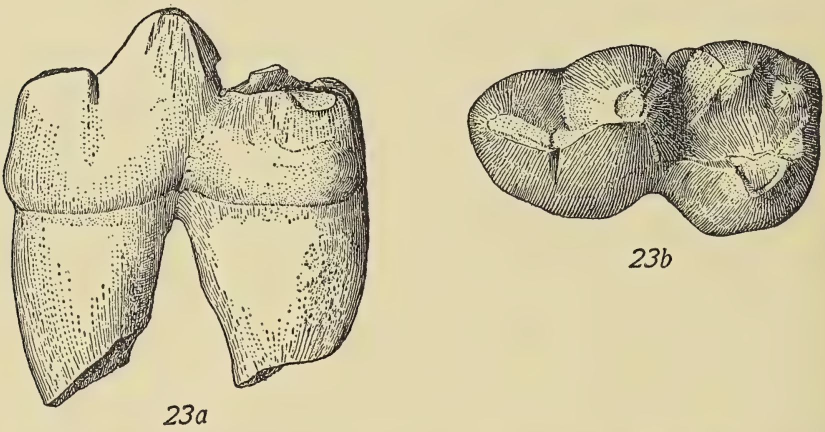
[5] Pilgrim, G. E., *op. cit.*, p. 227, 1914.

[6] Freudenberg, W., Geol. u. Palae., Abh. N. F., Bd. 9, p. 13, 1910.

[7] Lydekker, R., Mem. Geol. Surv. India, ser. 10, vol. 2, pl. 31, fig. 1, 1884.

The occurrence of the specimen from Tehuichila is presumably at a horizon not widely removed from that of the Rattlesnake Pliocene of Oregon, and there can be little doubt that, as suggested by Freudenberg, the form represents the general group of *Hyaenarctos*. The closer relationships can hardly be determined with certainty, but it is of great interest to note that this group is represented in beds of approximately lower Pliocene or late Miocene age in Mexico, adjacent to the South American region, in which the arctotheres were so largely developed in the Pleistocene.


23a

23b

FIGS. 23*a* AND 23*b*. *Hyaenarctos* or *Indarctos*. $M\bar{1}$, natural size. Fig. 23*a*, outer view; fig. 23*b*, occlusal view. From late Cenozoic deposits, Tehuichila, Mexico. (Drawn from cast furnished by Dr. W. Freudenberg.)

Two forms from South America described by Ameghino as *Pararctotherium* and *Proarctotherium* have been assumed to be ancestral types of the South American arctotheres. *Pararctotherium* is known from the Pampean formation, which corresponds to a considerable portion of the Pleistocene of North America. *Pararctotherium* is clearly a member of the *Arctotherium* group in which $M\bar{2}$ is considerably specialized. The anterior premolars of *Pararctotherium* are crowded, and the facial region was evidently shortened. There is no good reason for considering that this type is ancestral to *Arcto-*

therium; in fact, it may be one of the more specialized members of the *Arctotherium* group.

Proarctotherium is known from a very fragmentary specimen consisting of $M\bar{2}$ and $M\bar{3}$ from Parana. The Parana deposits have been assumed to be Pliocene, and may contain a small number of North American Pliocene types. Ameghino's[8] figure of the type specimen shows a $M\bar{2}$ not differing materially from that of *Arctotherium.* $M\bar{3}$ is large and elongate, approximating the form seen in typical Pleistocene *Arctotherium,* as in *A. simum.*

The type specimen of *Proarctotherium* evidently represents a typical member of the *Arctotherium* group. As the occurrence of a representative of the *Hyaenarctos* type seems now fairly established for the late Tertiary of Mexico, it is of course possible that a member of the group reached South America with the earliest of the Pliocene-Pleistocene emigrants from North America. While the characters of $M\bar{2}$ in the Parana form do not differ greatly from those of *Hyaenarctos,* $M\bar{3}$ is of a distinctly more advanced type. The nature of the specialization of $M\bar{3}$ is such as we commonly find associated with an anteroposteriorly elongated heel of the last upper molar, and is not to be expected in a Pliocene bear. Apparently the geologic occurrence of the Parana specimen must remain in doubt until other material of this nature appears in the Parana.

Transmitted October 25, 1916

[8] Ameghino, F., Contribucion al conocimiento de los mamiferos fosiles de la Republica Argentina, p. 319, pl. 21, fig. 1, 1889.

THE PLIOCENE RATTLESNAKE FORMATION AND FAUNA OF EASTERN OREGON, WITH NOTES ON THE GEOLOGY OF THE RATTLESNAKE AND MASCALL DEPOSITS

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    Pliohippus spectans (Cope).......... 632
    Milk dentition of Pliohippus.......... 635
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By John C. Merriam, Chester Stock, and C. L. Moody. *Carnegie Institution of Washington Publication No. 347*, paper III, pp. 43–92, October 8, 1925.

  - Hipparion occidentale Leidy.......... 641
  - Hipparion leptode Merriam or Hipparion occidentale Leidy.......... 643
  - Hipparion anthonyi Merriam.......... 644
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  - ? Teleoceras, near fossiger (Cope).......... 646
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INTRODUCTION

During the summer of 1916 a field party from the Department of Palaeontology, University of California, visited the type localities of Rattlesnake and Mascall formations on the John Day River in eastern Oregon. Five weeks were devoted to an examination of these later Tertiary deposits, primarily for the purpose of securing larger vertebrate collections from the two horizons. The lack of topographic maps and the necessity of spending much of the time in fossil collecting curtailed the geological observations that were made. The facts concerning the geology of the Rattlesnake and Mascall formations should be regarded, therefore, as constituting only a reconnaissance report. While the Mascall deposits yielded also mammalian remains, it seems desirable to reserve the consideration of the Mascall fauna for a later paper.

Since the expedition of 1916 small additions have been made to the collections from the Rattlesnake as a result of further work in the field.

PREVIOUS WORK

The stratigraphy of the John Day basin, including that of the Rattlesnake and Mascall formations, was discussed by J. C. Merriam[1] in 1901. In a later paper by J. C. Merriam and W. J. Sinclair[2] the known Tertiary faunas of the region were reviewed. The latter paper summarizes the results of faunal work in the John Day basin by former students and lists the assemblages of vertebrates from the various Tertiary horizons in this area. Only a small number of mammalian forms are definitely recorded in this paper from the Rattlesnake beds.

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[1] J. C Merriam, A contribution to the geology of the John Day Basin, Univ. Calif. Publ., Bull. Dept. Geol., vol. 2, pp. 269–314, 1901.

[2] J. C. Merriam and W. J. Sinclair, Tertiary faunas of the John Day region, Univ. Calif. Publ., Bull. Dept. Geol., vol. 5, pp. 171–205, 1907.

One of the results of the 1916 expedition to eastern Oregon was the discovery of remains of a hyaenarctid bear in the Rattlesnake beds. This material was described in 1919.[3] In a review of the Pliocene mammalian faunas from the Pacific Coast and Great Basin provinces, J. C. Merriam[4] gave a list of mammals comprising the Rattlesnake fauna, based principally on the collections made in 1916. Lastly, M. R. Thorpe[5] described the canid genus *Araeocyon* from material said to have been collected in the Rattlesnake and which is now in the Marsh collection at Yale University.

GEOGRAPHIC OCCURRENCE OF THE FOSSIL-BEARING FORMATIONS

The greater part of the field work of the 1916 party was carried on at the type localities of the Rattlesnake and Mascall formations, situated in Grant County, Oregon, near the point where the East Fork of the John Day River enters Picture Gorge. The region is approximately 5½ miles west of Dayville and occupies parts of townships 12S, R. 25 E., and 12S, R. 26 E., Willamette base line and meridian.

Observations of the 1916 expedition were limited to the region lying between Birch Creek and Canyon City. The entire drainage in this area is a part of the system of the East Fork of the John Day, which rises in one of the ridges of the Blue Mountains 30 or more miles to the east of Canyon City and flows in a general westerly direction to the vicinity of Dayville. The course from here to Picture Gorge, a distance of 5 miles, is northwest. At the gorge the river turns sharply to the north and flows in a nearly straight line to its junction with the North Fork at the north end of Turtle Cove. From the town of John Day to Picture Gorge the course of the East Fork is almost entirely within the soft tuffs of the Mascall formation. Only at the "iron bridge," midway between Mount

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[3] J. C. Merriam, C. Stock, and C. L. Moody, An American Pliocene bear, Univ. Calif. Publ., Bull. Dept. Geol., vol. 10, pp. 87–109, 1916.

[4] J. C. Merriam, Relationships of Pliocene mammalian faunas from the Pacific Coast and Great Basin provinces of North America, Univ. Calif. Publ., Bull. Dept. Geol., vol. 10, pp. 421–443, 1917.

[5] M. R. Thorpe, Two new fossil Carnivora, Amer. Jour. Sci., ser. 5, vol. 1, pp. 477–479, 1921.

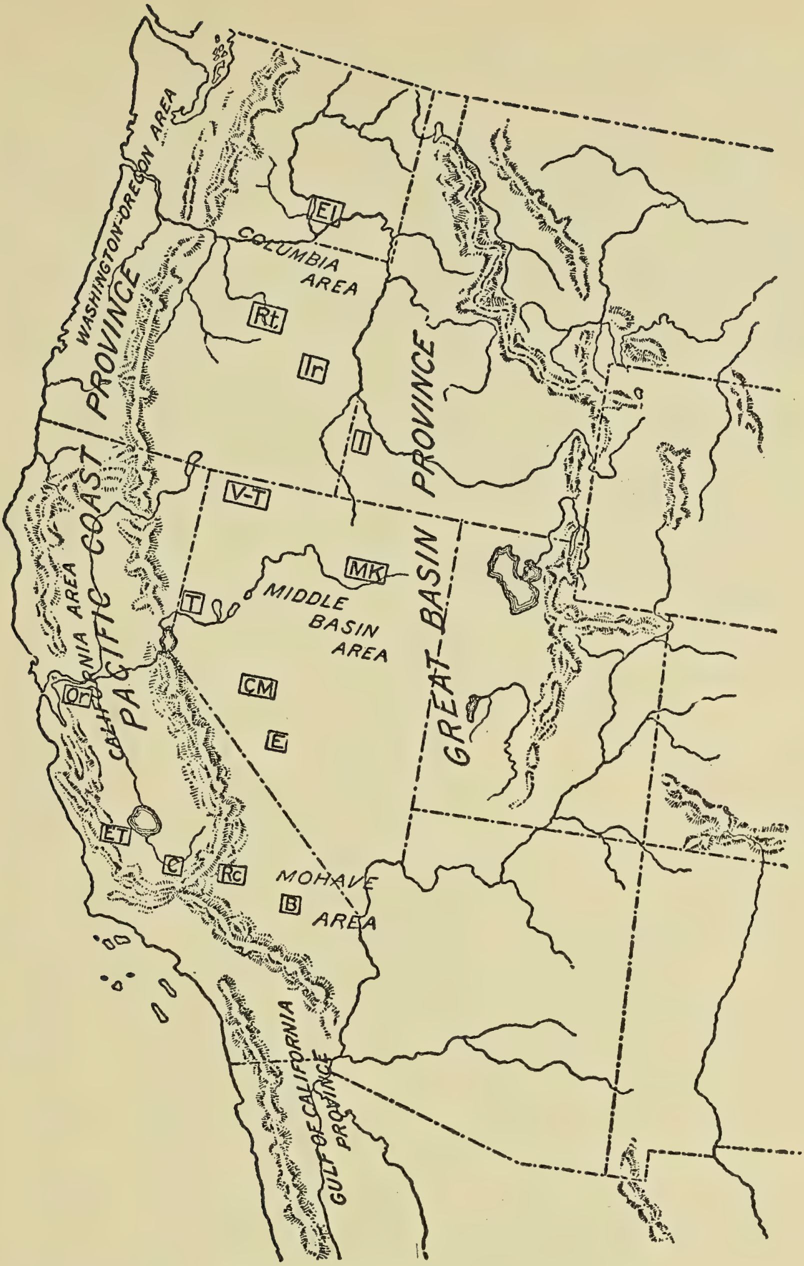
WASHINGTON-OREGON AREA
El
COLUMBIA AREA
Rt.
Ir
I
PACIFIC COAST PROVINCE
GREAT BASIN PROVINCE
V-T
MK
MIDDLE BASIN AREA
T
CALIFORNIA AREA
CM
E
Or
ET
C
Rc
MOHAVE AREA
B
GULF OF CALIFORNIA PROVINCE

FIG. 1. Outline map illustrating occurrences of Miocene and Pliocene mammal faunas in Tertiary provinces of the United States west of the Wasatch Range.

Rt, Rattlesnake Pliocene and Mascall Miocene
Ir, Ironside Pliocene
El, Ellensburg formation
I, Idaho beds
B, Barstow beds
VT, Virgin Valley and Thousand Creek beds
MK, McKnight Miocene
T, Truckee beds
CM, Cedar Mountain beds
E, Esmeralda beds
Or, Orinda-Pinole Tuff Pliocene
ET, Etchegoin Tulare beds and Merychippus zone
C, Chanac formation
Rc, Ricardo beds

Vernon and Dayville, where the country road crosses to the south bank, has the stream cut down to the underlying Columbia basalt. It thus pursues a subsequent course for 60 miles. At Picture Gorge, however, the river has cut a sharp, rugged canyon with nearly vertical walls rising 500 feet above the stream-bed, directly through a ridge of basalt. Picture Gorge, which takes its name from certain Indian pictographs on a cliff-exposure at the south end, is perhaps $1\frac{1}{2}$ miles long. The course of the river beyond the gorge to its confluence with the North Fork is through the so-called "Big Basin," the bedrock for the most part being in the John Day formation.

The chief tributary of the East Fork is the South Fork, which unites with the former at Dayville. The course of this stream is almost entirely within basalt or pre-Tertiary crystalline rocks. Cummings and Beach Creeks are the chief tributaries which drain the basalt ridge to the north of the East Fork. Streams to which frequent reference will be made in subsequent discussion are Cottonwood Creek, flowing from the south to meet the East Fork at Mascall Ranch; Rattlesnake Creek, entering the mouth of Picture Gorge, and Little Rattlesnake, its tributary; Rock Creek, which in its lower course closely follows the Mascall-basalt contact west of Picture Gorge; and Mountain and Birch Creeks, the main tributaries of Rock Creek. These streams all drain the region south and southwest of the sharp northern bend in the East Fork at Picture Gorge. Practically all the tributaries may be classed as perennial streams; in fact so dry is the summer climate that the John Day River in September shrinks to brook-like proportions.

A dominant control of the present topography within the East Fork valley is undoubtedly exerted by the Columbia lava, but of great importance in determining the local relief is a resistant rhyolite flow which occurs at a high horizon in the Rattlesnake formation. This serves as a protection to the easily reducible beds which lie at lower horizons, with the result that buttes determined by "rimrocks" are characteristic features of the physiography. In some cases, notably in the buttes north of Dayville, the gravels attain a considerable thickness above the rhyolite, while in others, particularly in the vicinity of the type section of the Rattlesnake, the lava alone forms the summit of the buttes. To the south of the main valley the rhyolite thins and gradually disappears, so that the hills in this direction take on a rounded and smooth appearance due to the ease with which the "loose" gravels of the Rattlesnake and the soft tuffs of the Mascall break down under the forces of erosion. These rounded hills, however, soon lead to mountains of considerable relief which constitute the divide between the John Day and Malheur drainage systems. The basalt and the crystalline pre-Tertiary rocks of this range give rise to a rugged topography which stands in marked contrast to the low relief of the rather even, rolling lava plateau bounding the valley of the East Fork on the north.

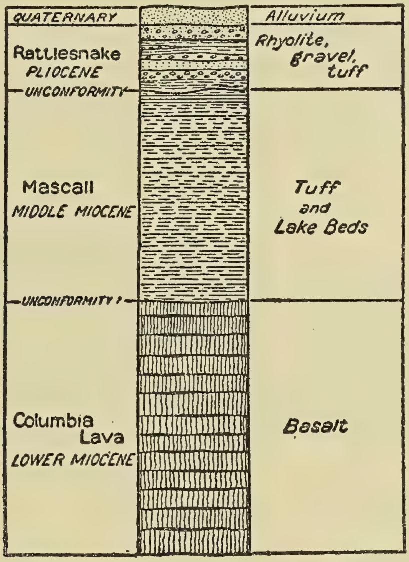
QUATERNARY
Alluvium
Rattlesnake
PLIOCENE
Rhyolite, gravel, tuff
UNCONFORMITY
Mascall
MIDDLE MIOCENE
Tuff and Lake Beds
UNCONFORMITY ?
Columbia Lava
LOWER MIOCENE
Basalt

FIG. 2. Columnar section showing formations occurring near type localities of Rattlesnake Pliocene and Mascall Miocene on Rattlesnake Creek, John Day Basin, Oregon.

GEOLOGIC SECTION AT TYPE LOCALITIES OF RATTLESNAKE AND MASCALL FORMATIONS

In the columnar section, figure 2, are given the formations occurring near the type localities of the Rattlesnake Pliocene and Mascall Miocene. Figure 3 sets forth the geologic relations of the formations at these localities.

MASCALL FORMATION

The Mascall formation is represented only in the synclinal depression in the Columbia basalt that extends along the John Day River from Canyon City westward for at least 50 miles. In no portion of this region are the Mascall beds present over an area more than 5 miles wide. A mile or two west of the junction of Mountain Creek with Rock Creek the Mascall is overlapped by the Rattlesnake gravels, so that it is not known to extend farther west than to the vicinity of Antone. The eastward limit of the formation is reached at Mount Vernon. The present distribution of the Mascall is evidently contingent upon the protection afforded the easily reducible tuffs by the basalt walls of the East Fork syncline. The formation was once undoubtedly of much greater extent, probably overlying a considerable part of the lava plateau north of the valley. Thus Collier[6] correlates the Dalles group with the Mascall and states that outliers of the latter are to be seen between Condon and the Columbia River. Exposures of the Mascall on Cottonwood Creek, on the south limb of the syncline, do not at all indicate marginal deposition, from which a former considerable southern extension may be inferred. South of the Blue Mountains exposures with a Mascall fauna are to be found over an extensive area.

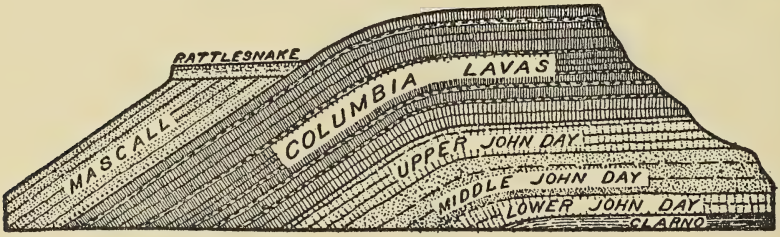

FIG. 3. Section showing geologic relations of Rattlesnake Pliocene and Mascall Miocene as exposed at type localities, John Day Basin, Oregon.

The relation of the Mascall beds to the Columbia lava is significant, as it has a very definite bearing upon the age of the vast lava fields of the northwest and hence upon the geologic history of the continent. Conditions in the vicinity of Picture Gorge are exceptionally favorable for a close determination of this important date, for here the John Day beds bearing an upper Oligocene fauna underlie the lava with a possible erosion period intervening. Directly above the basalt appears the Mascall formation, which yields a middle Miocene mammalian fauna.

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[6] A. J. Collier, The geology and mineral resources of the John Day region, Oreg. Bur. Mines and Geol., Mineral resources of Oregon, vol. 1, No. 3, p. 19, 1914.

Consideration of the period of extravasation of the lava is contingent not only upon the recognition of Oligocene age for the John Day and middle Miocene age for the Mascall, but also upon the assumption of conformity between the Mascall and the basalt.[7] Certain observations tend to indicate that an interval of erosion and possibly a local deformation of the lavas may have occurred before the accumulation of the Mascall tuffs. This evidence is based upon a local variation of Mascall sediments along the strike in company with frequent changes in thickness below a known persistent horizon in the tuffs.

In the rhyolite-covered butte west of Picture Gorge the basal member of the Mascall is a coarse, slightly concretionary, very yellowish tuff bearing occasional small blocks of basalt. West of McDonald's ranch, at the union of Birch Creek and Rock Creek, 4 miles from Picture Gorge, a section of the Mascall is exposed which possesses at least three thick members unknown in the type section. All of these strata are below a massive, white, earthy tuff, termed in the field the "mammal horizon" because of its comparative richness in fossil vertebrate material. The sediments near the McDonald ranch are (*a*) a series of red tuffs approximating 100 feet in thickness, (*b*) a grayish-blue sand bearing occasionally dark carbonaceous beds, 50 feet, and (*c*) a very light, pithy, thin-bedded shale of a walnut-brown color, bearing frequent impressions of stems and occasional rude traces of leaves. The latter member may reach a thickness of 40 feet. On the east side of the John Day River, opposite the Mascall ranch house, appear plant-bearing shales and gypsiferous strata at apparently a lower horizon than is found at the type section. It would thus appear that the surface on which the Mascall sediments accumulated was at least locally irregular. It is probable that the lava now exposed on the west wall of Picture Gorge formed a low hill at the beginning of Mascall time and that the plant-bearing beds were deposited on its flanks in lacustrine basins. The suggestion of pre-Mascall disturbances of the basalt consists in the fact that the present south surface of the basalt slope north of the East Fork, which seems to pass under the Mascall beds, truncates the individual flows of lava exposed in Picture Gorge. This truncation is expressed in the topography of the slope by a step-like appearance, occasioned by the wearing back of certain less-resistant lava beds due to sapping action of the softer tuffs intercalated between the flows. If these conditions are considered sufficient evidence upon which to base an unconformity, then the period of extravasation of the lavas must be somewhat earlier in the early middle or lower Miocene.

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[7] A. J. Collier, *ibid*, p. 17, 1914.
J. C. Merriam, Univ. Calif. Publ., Bull. Dept. Geol., vol. 2, p. 306, 1901.

The vertebrate remains of the Mascall were obtained at a single horizon, so that a definite datum plane appears to which other horizons may be referred. This is a massive, white, earthy tuff with no trace of bedding planes. It fractures irregularly into great blocks which soon disintegrate, leaving a vertical or overhanging wall, from 20 to 50 feet high. An important element in the preservation of this wall is a hard, yellowish, concretionary tuff, which immediately overlies the earthy fossiliferous zone and weathers into very rough surfaces. These two beds, the concretionary tuff and the earthy tuff, are the most persistent of all members of the Mascall formation. Their characters are very constant and a number of exposures are to be found from the lava-topped buttes of the type section eastward to Wilson's ranch, a distance of about 12 miles. The "mammal horizon" forms the white bluff in the butte of the type section; its dip of 18° carries it to the level of Rattlesnake Creek at this point, where it appears as the south bank of that stream. The outcrop then pursues a straight line to the Mascall ranch house, appearing in the south bank of the John Day River. Near Mascall's house the beds are covered by terrace deposits and from here to Dayville the outcrops are concealed under Recent and Pleistocene deposits of the river. At Dayville, however, the tuffs are again evident on the north side of the John Day, where they appear somewhat nearer the base than at the type locality, although they are otherwise identical in character with the beds at the Mascall ranch. The strike carries the horizon across the river somewhat below MacRae's ranch. Two miles east of its appearance on the south bank of the river the horizon passes under Rattlesnake gravels and does not reappear to the east. In this last exposure the admixture of siliceous shale with the concretionary tuff layer, and also subordinately with the earthy tuff, indicate marginal lacustrine conditions.

The section from the "mammal horizon" to the base of the formation, immediately to the west of Picture Gorge, consists of alternating yellowish and grayish tuffs. The variations in the basal members of the tuff series east of Picture Gorge and on Rock Creek west of McDonald's ranch have already been mentioned. In the vicinity of Belshaw ranch, 12 miles east of Dayville, the basal portion of the Mascall is lithologically different from the lower horizons of the section farthest west. Sandstones and thick-bedded, white tuffaceous shales bearing numerous, well-preserved plant remains and occasional fish remains replace the coarse yellow tuffs of the type section and the carbonaceous beds of Rock Creek. Particularly prominent is a bluish-gray, medium-grained, massive sandstone which overlies the plant-bearing strata and weathers into fantastic pinnacles and crags on dip outcrops and into irregular, cavernous openings in cliff sections. A sandstone of this peculiar character overlies the "mammal horizon" immediately north of MacRae's ranch, 3 miles east of Dayville. Indications are thus that the plant-bearing beds near the Belshaw ranch are not far from the horizon of the fossiliferous tuffs in the vicinity of the Mascall ranch. On the south side of the John Day in the vicinity of the Belshaw ranch, the Mascall formation contains several horizons of cross-bedded sandstones, grits, and conglomerates, the material of which was derived not from the Columbia lava, but apparently from pre-Tertiary rocks of the region to the east.

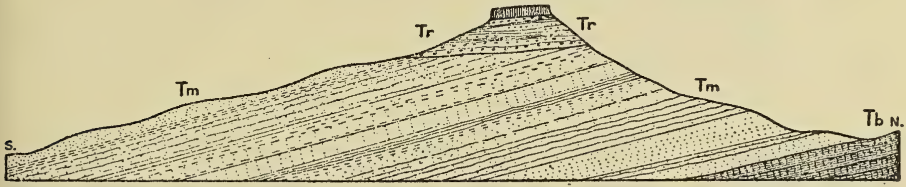

FIG. 4. Section through Tertiary formations near type localities of Rattlesnake Pliocene and Mascall Miocene. *Tb*, Columbia basalt; *Tm*, Mascall; *Tr*, Rattlesnake.

Above the "mammal horizon" the Mascall beds at the type section are chiefly light-colored tuffs of medium to fine grain. Rarely, as at the Mascall outcrop on the second butte west of Picture Gorge, small lenses of fine gravel appear intercalated with the tuffs. Plant remains were found at two horizons above the mammal-bearing beds. The first occurrence was in a brownish shale alternating in thin layers with a grayish-blue sandstone, 200 feet above the mammal horizon. The second plant locality was found 1,000 feet above the first in a bluish-gray, arenaceous shale.

The following columnar section was observed at the type locality of the Mascall formation west of Picture Gorge:

		Feet
1.	Uppermost deposit. Gray, yellow, and brownish tuffs	400
2.	Bluish-gray, arenaceous shale. Leaf impressions	2
3.	Medium-grained, yellowish, grayish, reddish, and greenish tuffs, with occasional gravel lenses	600
4.	Brownish shale finely interbedded with bluish sandstone. Leaf impressions	5
5.	Yellowish, medium-grained tuff	200
6.	Concretionary, yellowish tuff giving rugged outcrops and rough surfaces	20
7.	Massive earthy tuff breaking irregularly and forming bluff-outcrops. Mammal horizon	30
8.	Alternating yellowish, reddish, and grayish fine-grained tuff	110
9.	Bluish, fine pumiceous sand	3
10.	Earthy, white tuff	20
11.	Medium-grained, yellowish and grayish tuffs alternating	650
12.	Basal deposit. Yellowish tuff with basalt blocks up to a foot in diameter	50
	Total	2,090

A poor grade of lignitic coal has been found in lower horizons of the Mascall at various localities in the valley of the East Fork. Basalt of an olivine-free type[8] is found interbedded with Mascall tuffs within the basin of Rock Creek. The flows are lenticular and do not reach as far east as Picture Gorge. The basalt exposed on Rattlesnake Creek and Birch Creek has been brought into its present position by a small strike fault.

GEOLOGIC RELATIONS OF RATTLESNAKE FORMATION

Unconformably overlying the Mascall beds throughout the basin of the East Fork is an extensive series of gravels and tuffs with an intercalated bed of rhyolite, constituting the Rattlesnake formation. The Rattlesnake occasionally overlaps the Mascall and lies directly upon the basalt; from Antone to Mitchell it lies successively upon basalt, pre-Tertiary, and Clarno; on the south side of the John Day River from the "iron bridge," 8 miles east of Dayville, to Canyon City, it rests upon crystalline rocks of pre-Tertiary age. The Rattlesnake is not certainly known outside the basin of the East Fork, although rhyolite similar to that characterizing the formation is known from the Crooked River region.[9] It is evident that the northern limit of the formation was not far from its present extent in the valley of the East Fork, for in the vicinity of Picture Gorge and in the area from Dayville to Mount Vernon, the rhyolite, lying almost horizontal, abuts upon dip slopes of the basalt with a southerly inclination of 18°. The southern extension was probably somewhat greater than it is at present. The gravels thicken markedly south of the river. This is especially noticeable on Cottonwood Creek and in the hills southwest of Dayville. The rhyolite wedges out on the west side of Cottonwood, and appears as a thin stratum of reddish ash in the large triangular outcrop facing Dayville on the southeast. It would thus appear that the rhyolite was poured out over an ancient flood-plain of the John Day River, and that it never extended laterally beyond this limit.

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[8] F. C. Calkins, A contribution to the petrography of the John Day basin, Univ. Calif. Publ., Bull. Dept. Geol., vol. 3, pp. 165–166, 1902.

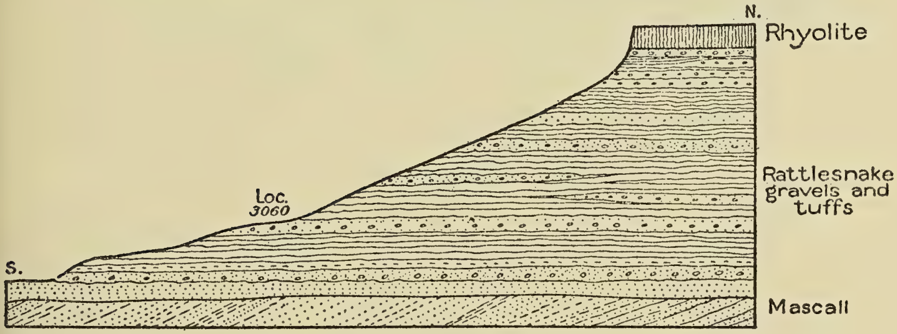

FIG. 5. Section showing relationship of Rattlesnake rhyolite, gravels, and tuffs to the Mascall formation. Note stratigraphic position of U. C. vertebrate fossil locality 3060.

The area of Rattlesnake exposed in the butte west of Picture Gorge has generally been termed the type section, and although it really represents but a small part of the entire succession within the formation, it was subjected to more careful study than elsewhere, due to the presence of mammalian fossils in the tuff and in the gravel. Great local variations occur in the sedimentary portion of the formation. Beds of coarse gravel frequently alternate with the finest earthy tuffs; lenses of one type of clastic material are abundantly included within those of another type, and occasional transitions of the fine tuff into gravel are to be noted along the strike. The following columnar section was measured west of the saddle dividing the two areas of rhyolite at the type locality:

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[9] I. C. Russell, Preliminary report on the geology and water resources of central Oregon, U. S. Geol. Surv. Bull. 252, pp. 59–60, 1905.

C. Stock and E. L. Furlong, Univ. Calif. Publ., Bull. Dept. Geol., vol. 13, p. 312, 1922.

		Feet
1.	Summit of section. Rhyolite. Massive flow with tuffaceous phases, irregular beds of lapilli near base, pumiceous fragments throughout	28
2.	Rhyolitic débris. Surface shows abundance of round basaltic pebbles	120
3.	Gravel, cross-bedded sandstone, and thin lenses of brownish tuff	15
4.	Brown, earthy tuff with concretions	5
5.	Medium-grained grit in lenticular masses	3
6.	Cross-bedded sandstones, brown earthy tuff with irregular concretions, well indurated. Locality 3060 U. C., with *Pliohippus*, *Prosthennops?*	9
7.	Brown and yellowish tuff and gravel	14
8.	Tuff, cross-bedded sandstone, and basaltic gravel interdigitating	25
9.	Massive, buff tuff with several indurated layers. Locality 3235 U. C., with *Teleoceras*	17
10.	Rounded, basaltic gravel	11
11.	Buff tuff	3.5
12.	Basaltic gravel, well-rounded and sorted	4.5
	Total	255

Without exception the pebbles in the gravel at the type locality show much evidence of continued water-wear; the majority of them may be termed "well-rounded." Petrographically the pebbles are identical with the Columbia basalt and it is practically certain that the great lava sheet has been the source of the coarser detrital material of these beds. Closely associated with the gravels are cross-bedded, rather quartzose sandstones and somber-colored tuffs. The sources of these materials are not definitely known, but it seems probable that the sandstones have been derived from the area of crystalline rock southeast of Picture Gorge, while the tuffs may represent the finer material of volcanic eruption, transported to its present position in part by winds and in part by the Tertiary stream on whose flood-plain the gravels were accumulating. The possibility that the tuffs may in part represent reworked Mascall sediments must not be overlooked.

The induration of some of the Rattlesnake beds is extreme; both gravel and tuff may be locally very hard. The sixth and tenth members of the columnar section given above are particularly well cemented by the infiltration of silica and carbonate of lime.

In general the Rattlesnake west of Picture Gorge has been eroded down to the rhyolite flow. A perfectly even, gently sloping surface appears continuously from the butte of the type section to a point several miles beyond Birch Creek; the rhyolite throughout this extent is a "rim-rock" with vertical walls from 10 to 50 feet in height. On Cottonwood Creek and in practically all Rattlesnake areas east of Picture Gorge, however, a very considerable thickness of gravels overlies the rhyolite. On Cottonwood Creek the gravels above the rhyolite are 450 feet thick, and although olivine basalt, evidently derived from the Columbia flows, forms by far the largest number of pebbles of the coarser beds, other pebbles appear in abundance. Granitic and quartz pebbles are not at all uncommon, while rhyolite fragments of a character identical with that of the

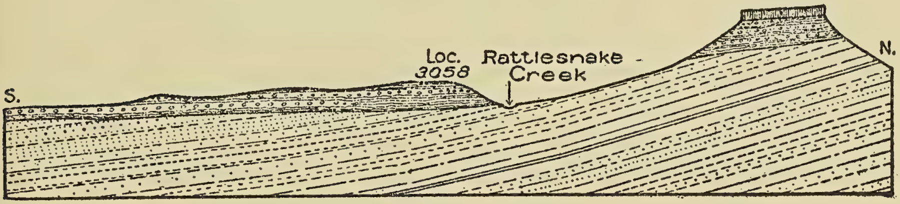

Fig. 6. Section across Rattlesnake Creek, showing relationship of Rattlesnake formation to Mascall deposits and position of U. C. vertebrate fossil locality 3058 in the Rattlesnake.

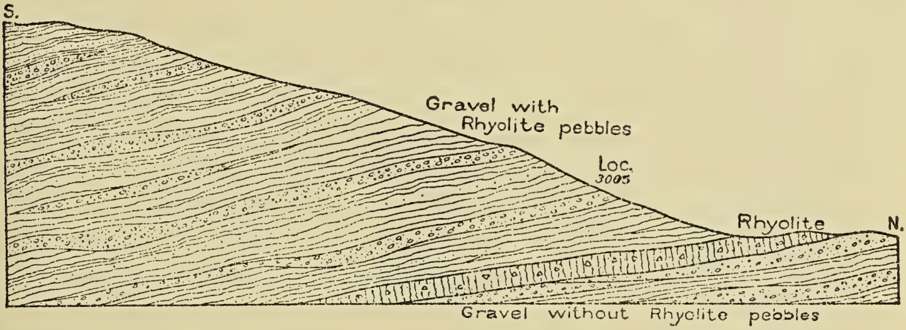

Fig. 7. Section of Rattlesnake formation exposed on Cottonwood Creek, showing particularly gravel with rhyolite pebbles resting on rhyolite and position of U. C. vertebrate fossil locality 3065.

rhyolite flow of the Rattlesnake are frequently to be observed. Tuffs interbedded with the gravels above the rhyolite indicate that there is no great lapse of time between the upper and lower horizons of the formation. North of Dayville the upper gravels are developed to a maximum thickness of 200 feet; at Mount Vernon they are less than 100 feet thick.

The rhyolite flow which characterizes the Rattlesnake throughout its extent varies in thickness up to 50 feet. The wedging out of the flow on the south side of the river has been mentioned. From Dayville to Mount Vernon no rhyolite is known on this side of the river, but "rim-rocks" of the characteristic brownish-red lava are common south of the stage road leading from Mount Vernon to Canyon City. The rhyolite is always massive and bears no traces of fluxion lines or other banding common to acid lavas. It breaks with conchoidal fracture on a large scale. Commonly great irregular columns averaging 20 feet across are produced on the margins of the "rim-rocks." On weathered surfaces the rhyolite is uniformly of a reddish-brown color, but on freshly broken surfaces it appears bluish-gray. Phenocrysts are limited to occasional small, untwinned feldspars; the greater part of the rock is felsitic. Angular lapilli and fragments of pumice are abundant throughout the lava and may be so concentrated locally that the felsitic matrix nearly disappears. Near the base of the rhyolite, pebbles from the underlying gravels are frequently seen in little black pockets in the grayish lava. In the vicinity of Mount Vernon on Beach Creek unusual jointing phenomena are to be observed in the rhyolite. Columnar structure of a radial type is perfectly developed, producing stony rosettes of large size. The center of the rosette structure is usually near the middle height of the flow, which is 40 feet thick in this region. The columns are well formed and extend to the upper and lower limits of the flow, with an average diameter of 15 inches. About 2 miles southwest of the Wilson ranch and 5 miles east of Dayville, a remarkable exposure of Rattlesnake gravel occurs lying on northerly dipping basalt. These gravels form vertical cliffs, estimated as at least 200 feet in height, and weather into picturesque crags and pinnacles. The horizon of the rhyolite flow was not recognized in this exposure, and it may be that neither the lava nor its acid tuff extended so far south. The formation at this point is estimated to be 400 feet thick.

The maximum thickness encountered in the Rattlesnake was on Cottonwood Creek, where the formation from the basal beds to the top of the upper gravels reaches a thickness of 900 feet.

The surface upon which the Rattlesnake gravels and tuffs accumulated was apparently one of considerable relief, though perhaps of gentle contour. At Picture Gorge not over 50 feet of gravels separate the rhyolite flow from the basalt, while on Cottonwood Creek from 400 to 500 feet of tuffs and gravels lie below this horizon. This represents a thickening of from 350 to 450 feet in a distance of less than 2 miles. The Rattlesnake-Mascall contact in the type section dips decidedly toward the south, and, as the Rattlesnake beds are very slightly disturbed, this becomes an index of pre-Rattlesnake relief. The unconformity between the Rattlesnake and Mascall is one of the most clear-cut geologic features of the John Day basin; the discordance of dip varies from 6° to 15°, and the sharp distinction in the two types of sediments usually permits an easy delimitation of the formations.

STRATIGRAPHIC POSITION OF HIPPARION

The genus *Hipparion* has at various times been listed with the fauna of the Mascall, but results of the present investigation sustain the conclusion, suggested by Merriam and Sinclair,[10] that this form is confined to the Rattlesnake formation. Careful search throughout the type locality of the Mascall failed to reveal more than one

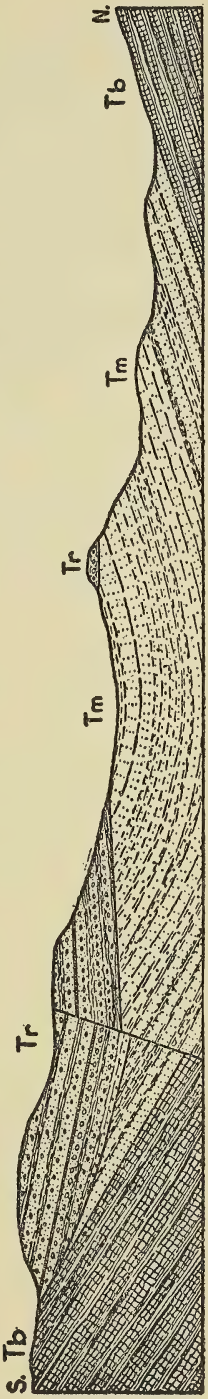

FIG. 8. Diagrammatic section showing faulting and relationship of beds on Birch Creek, Grant County, Oregon. *Tb*, Columbia basalt; *Tm*, Mascall; *Tr*, Rattlesnake.

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[10] J. C. Merriam and W. J. Sinclair, Tertiary faunas of the John Day region, Univ. Calif. Publ., Bull. Dept. Geol., vol. 5, p. 198, 1907.

zone yielding mammalian remains. This horizon is in the type section, approximately 900 feet from the base of the formation. Localities from which Mascall fossils have been collected west of Rattlesnake Creek on the road to Antone, and in the vicinity of Birch Creek, are in this horizon, but have been brought to their present position by post-Rattlesnake faulting. Fossils were frequently found in place in this "mammal horizon" at numerous points between Birch Creek and MacRae's ranch, a distance of 15 miles, but in no case was a horse, more advanced than *Merychippus*, found embedded in the tuff. On the other hand, *Hipparion* was found once actually in place in Rattlesnake tuff and was frequently discovered with *Pliohippus* lying on Rattlesnake gravel and tuff. All known occurrences of *Hipparion* were on or beneath Rattlesnake exposures. Under these conditions the occasional occurrence of a tooth of *Hipparion* resting on Mascall tuff would not seem to negative the evidence indicating restriction of this group to the Rattlesnake formation in this region.

Structure

The valley of the East Fork of the John Day River as far down as Picture Gorge appears to be a long, narrow syncline determined by a rather sharp flexure in the Columbia lava and the Mascall tuffs. This structural trough is of variable width, but never exceeds 5 miles in lateral dimension; its length is disproportionately great, being at least 50 miles. In the vicinity of the type section both limbs of the syncline are basalt, but pre-Tertiary rocks appear as the south limb, both east and west of a basalt outcrop of approximately 12 miles in length. The dip on the north limb of the syncline does not vary greatly from 18°, while on the south limb, as seen along Cottonwood Creek, the basalt dips 30° north. Merriam[11] mentions exposures, reported to be lava, in nearly vertical position high up on the southern slope. Collier[12] reports the lava as vertical "at Flat Creek about 8 miles east of the Picture Gorge locality and 1 mile south of the John Day River."

Faulting has affected the valley of the East Fork, but it is rather subordinate as a structural feature. Faults are to be seen in section on Birch, Rattlesnake, and Cottonwood Creeks. The diagrammatic section (fig. 8) shows the relations found on Birch Creek. The rhyolite of the Rattlesnake is here vertically displaced through a distance of 200 feet, the north side of the fault being the downthrown side. On Rattlesnake Creek basalt is exposed by faulting, but the actual throw is not at this point determinable. On Cottonwood Creek the rhyolite is displaced vertically 100 feet, but here the down-throw is on the south side of the fault. These exposures are apparently on the same fault. Thus there seems to be indicated a motion on the fault-plane resulting in an uplift on the north side with a rotation in an east-west direction, this secondary tilting being to the west.

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[11] J. C. Merriam, Univ. Calif. Publ., Bull. Dept. Geol., vol. 2, p. 305, 1901.

[12] A. J. Collier, Ore. Bur. Mines and Geol., Mineral Resources of Oregon, vol. 1, No. 3, p. 17, 1914.

Age and Relationships of the Rattlesnake Fauna

The Rattlesnake fauna has unusual significance owing to exceptional clearness of stratigraphic relations of the beds in which it occurs. As indicated in the discussion of the geology of the fossil-bearing beds at the type localities of the Rattlesnake and Mascall, the Rattlesnake formation rests in marked unconformity upon the Mascall, which contains a mammalian fauna of middle or upper Miocene age. Through the accumulated Rattlesnake deposits deep cañons have been cut, and in the lower reaches of these excavations are deposits containing a Pleistocene fauna. The age of the Rattlesnake formation is therefore limited on one side by a period of erosion and deformation succeeding accumulation of the Mascall Miocene, and on the other side by a period of erosion preceding accumulation of deposits of Pleistocene age.

The following list of mammals, representing the Rattlesnake fauna, is based chiefly on materials collected in these deposits by the expedition of 1916:

Rattlesnake Fauna

- Carnivora:
  - Canis?, cf. davisi Merriam.
  - Amphicyonid or Ursid sp.
  - Indarctos (?) oregonensis Merriam, Stock, and Moody.
  - Indarctos (?) sp.
  - Mustela n. sp.
  - Felid sp. A, large.
  - Felid sp. B, small.
- Rodentia:
  - Otospermophilus gidleyi n. sp.
- Lagomorpha:
  - Hypolagus, near vetus (Kellogg).
- Edentata:
  - Megalonychid? gen. and sp. indet.
- Proboscidea:
  - Proboscidean remains.

Equidae:
  Pliohippus spectans (Cope).
  Hipparion sinclairi (Wortman).
  Hipparion occidentale Leidy.
  Hipparion leptode Merriam or Hipparion occidentale Leidy.
  Hipparion anthonyi Merriam.
Rhinocerotidae:
  ? Teleoceras, near fossiger (Cope).
Suidae:
  Prosthennops? sp.
  ?Platygonus rex Marsh.
Camelidae:
  Pliauchenia? or Alticamelus?
Bovidae:
  Sphenophalos sp.
  Ilingoceros or Sphenophalos? sp.

The fauna of the Rattlesnake deposits is widely removed from the mammalian assemblage known from the Mascall Miocene and from the Virgin Valley fauna. It is also distinctly separated from such upper Miocene faunas known in the Great Basin province as the Barstow and the Cedar Mountain. There is certainly a closer relationship between the Rattlesnake and Ricardo faunas than exists between the latter and either the Barstow or the Cedar Mountain fauna. The Ricardo is generally regarded as being of lower Pliocene age.

A comparison between the Rattlesnake fauna and that of the Ricardo suggests that the former is more advanced. The horses of the Rattlesnake include *Pliohippus* and *Hipparion*, genera that are known also from the Ricardo. In size and in complexity of the enamel pattern of the cheek-teeth some of the Oregon hipparions seem not far removed from *Hipparion mohavense* of the Ricardo Pliocene. On the other hand, material is available representing types larger than *H. mohavense*, and at least one form is known, namely, *Hipparion anthonyi*, in which a stage of complication of enamel pattern in the cheek-teeth is reached which exceeds that found in the typical *Hipparion* from the Ricardo beds. Among the artiodactyls we should note the contrast between the forms of *Merycodus* from the Ricardo and the larger antelopes related to *Sphenophalos* and *Ilingoceros* of the Rattlesnake fauna. The faunal difference between the Rattlesnake and Ricardo may be due to geographic variation or to earlier appearance in the northern region of the Great Basin province of immigrants reaching North America in Pliocene time. It is probable that the difference between the Rattlesnake and Ricardo faunas is due in part to difference in stage of evolution, with the Ricardo as the earlier stage. It is not probable that the difference amounts to more than a small portion of a geologic period.

Comparison between the mammalian assemblages from the Rattlesnake and from the Thousand Creek of Nevada suggests that the Rattlesnake fauna makes a somewhat nearer approach to the Thousand Creek than does the Ricardo. Species of *Pliohippus* and *Hipparion* occur also at Thousand Creek, and one form, *Hipparion leptode*, seems rather closely related to a type of horse from the Rattlesnake. In both the Rattlesnake and Thousand Creek faunas the genus *Merycodus* is absent, or at least is not known by available materials at the present time, while larger antelopes of the *Sphenophalos* and *Ilingoceros* types are present.

The *Pliohippus* forms among the horses of the Rattlesnake are much like those from the *Pliohippus coalingensis* zone of the Etchegoin in the Pacific Coast province, while *Hipparion* species in the Oregon fauna show some resemblance to a species from the Hipparion zone of the Pacific Coast province. Antelope remains from the Orinda-Pinole Tuff Pliocene near Pinole, California, bear some resemblance to types known from the Rattlesnake and Thousand Creek horizons.

Description of Fauna

CARNIVORA

Canis? cf. davisi Merriam

A fragment of a lower jaw, No. 22384, containing a lower carnassial (fig. 9) from U. C. locality 3048 of the Rattlesnake formation represents a canid type similar to one very imperfectly known from the Pliocene of the Great Basin region. The metaconid has approximately the size of that in the timber wolves of the *Canis* group. The heel is shorter, but not relatively shorter, than in the timber wolves, and the hypoconid is large. The entoconid region is imperfectly preserved, but this tubercle was apparently very small in comparison with the size of the hypoconid. No. 22384 may represent an amphicyonine or may belong to a type which has been referred to as *Canis? davisi*, known from the Thousand Creek Pliocene of Nevada.

Measurements (in Millimeters) of No. 22384

$\overline{M1}$, greatest antero-posterior diameter	23.8
$\overline{M1}$, greatest transverse diameter across metaconid	10

Amphicyonid or Ursid sp.

A fragment of a lower jaw, No. 22462 (fig. 10), from U. C. locality 3045 in the Rattlesnake formation, contains a single molar tooth situated immediately in advance of the base of the coronoid process. There is no alveolus of the tooth posterior to the individual present and a portion of the alveolus anterior to this tooth shows a narrow posterior root resembling the form of posterior root of M$\bar{2}$ more closely than that of M$\bar{1}$ accompanying tubercular molars as distinctly of a crushing type as the molar in No. 22462. The tooth present is either M$\bar{3}$ or M$\bar{2}$. It shows a form corresponding in general to that of M$\bar{2}$ of the bears. In the trigonid portion the

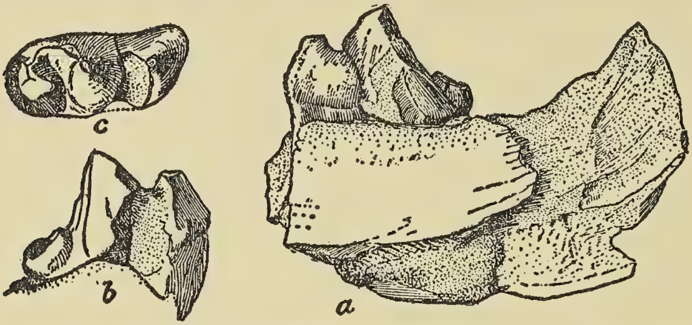


Fig. 9. *Canis?* cf. *davisi* Merriam. M$\bar{1}$, No. 22384 U. C. C.; *a*, inner view; *b*, outer view; *c*, occlusal view; ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

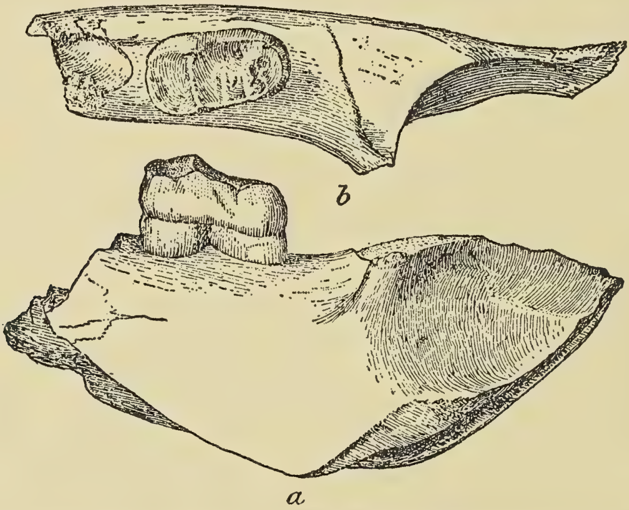


Fig. 10. Amphicyonid or Ursid sp. Fragment of jaw with inferior molar tooth, No. 22462 U.C.C.; *a*, outer view; *b*, occlusal view; ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

protoconid and metaconid are small, very low, and are connected lightly by a transverse ridge. Anterior to the protoconid and metaconid there is a wide shelf approximating in area that anterior to the protoconid and metaconid of the bears, but no distinct paraconid is shown. The posterior or talonid region of the tooth is large and the tubercles are very low.

This tooth does not correspond to any M$\bar{3}$ known to the writers in either the ursid or canid group. The characters possessed by this specimen are strikingly similar to those of M$\bar{2}$ of the bears, but there is no suggestion of an alveolus of M$\bar{3}$ and no member of the bear group from the Tertiary has a M$\bar{3}$ as advanced as this tooth. The molar is somewhat longer antero-posteriorly and relatively narrower than M$\bar{2}$ of *Ursavus*, and is also larger than any *Ursavus* form known to the writers. The tooth in No. 22462 is longer antero-posteriorly, narrower, and more specialized for the exclusive function of crushing than in M$\bar{2}$ or M$\bar{3}$ of the *Amphicyon* forms known to the writers. This tooth approaches in some respects M$\bar{2}$ of *Simocyon*, but is is somewhat larger and the talonid region is more fully developed. With M$\bar{2}$ of *Simocyon* the specimen represented by No. 22462 has in common the fact that there is no evidence of another tooth posterior to it.

Amphicyon sinapius Matthew[13] from the Colorado Loup Fork has a more typical Amphicyon-like form, and the heel region is entirely different from that of this species.

Amphicyon amnicola Matthew and Cook[14], described from the Snake Creek beds, is a large form with large and broad M$\bar{2}$ and a large two-rooted M$\bar{3}$. As nearly as can be judged M$\bar{3}$ of *Amphicyon amnicola* had dimensions close to those of the molar tooth represented in the specimen from the Rattlesnake. It is possible that No. 22462 is related to the Snake Creek species. It is necessary to await the discovery of additional material before forming a final judgment as to the affinities of this form.

MEASUREMENTS (IN MILLIMETERS) OF NO. 22462, M$\bar{2}$ OR M$\bar{3}$

Antero-posterior diameter	18.8
Greatest transverse diameter	10.5
Antero-posterior diameter of trigonid	12.1
Antero-posterior diameter of talonid	6.7
Width of lower jaw at anterior base of coronoid process	19

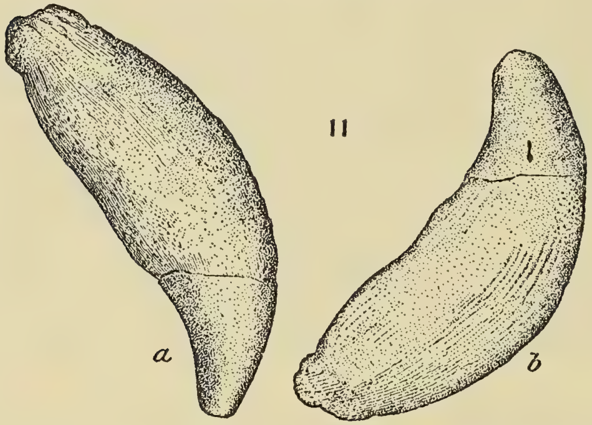
[13] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 16, p. 288, 1902.

[14] W. D. Matthew and H. J. Cook, Bull. Amer. Mus. Nat. Hist., vol. 26, p. 368, 1909.

Indarctos (?) oregonensis Merriam, Stock, and Moody

Indarctos (*?*) *oregonensis* Merriam, Stock, and Moody, Univ. Calif. Publ., Bull. Dept. Geol., vol. 10, pp. 87–109, 1916.

Type Specimen.—No. 22362, University of California collections in Museum of Palaeontology. Specimen from Rattlesnake beds located near center of N.W.¼, sec. 30, T. 12 S., R. 26 E., Willamette base line and meridian, Grant County, Oregon, approximately 5½ miles west of Dayville, and not over three-quarters of a mile south of type section of Rattlesnake formation.



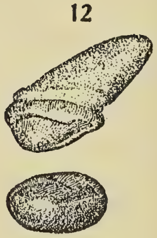


Fig. 11. *Indarctos* (*?*) *oregonensis* Merriam, Stock, and Moody. Canine teeth, No. 22362 U.C.C.; *a*, upper canine; *b*, lower canine; lateral views. ×0.50. Rattlesnake Pliocene, John Day Valley, Oregon.

Fig. 12. *Indarctos* (*?*) *oregonensis* Merriam, Stock, and Moody. P$\underline{1}$, No. 22362 U.C.C.; inner and occlusal views. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

Material available of type specimen includes I$\underline{2}$, I$\underline{3}$, superior and inferior canines, P$\underline{1}$, P$\underline{4}$, M$\underline{2}$, M$\overline{2}$, an atlas, the greater part of humerus, half of ulna, metacarpal V, navicular, cuboid, metatarsal II, and several phalanges.

Dentition.—The incisors, canines, and P$\underline{1}$ (figs. 11 and 12) approach in their characters the corresponding teeth in *Arctotherium*. The upper carnassial differs markedly from all specimens of *Ursus* and *Arctotherium* known to the writers, and approaches closely the type of P$\underline{4}$ known in the several species of *Hyaenarctos*. In the Oregon species the paracone is slightly larger than the metacone. The protocone is very large, approximating in its cross-section the size of the paracone, and is situated so far forward that its anterior border is not posterior to the corresponding border of the paracone as in *Ursus* and *Arctotherium*. A large parastyle is present. The tooth is distinctly three-rooted, a large and widely divergent root supporting the protocone. The outer contour of the tooth shows a distinct concavity of the cingulum opposite the posterior side of the paracone.

P$\underline{4}$ (fig. 13) differs from the corresponding tooth of *Arctotherium* in the relatively large size of the protocone; in the support of the protocone upon a distinct, widely diverging inner or third root; in the situation of the protocone as far forward as the paracone; and in the presence of a large, distinctly separated parastyle. In all of the characters in which this tooth differs from *Arctotherium* it resembles *Hyaenarctos*.

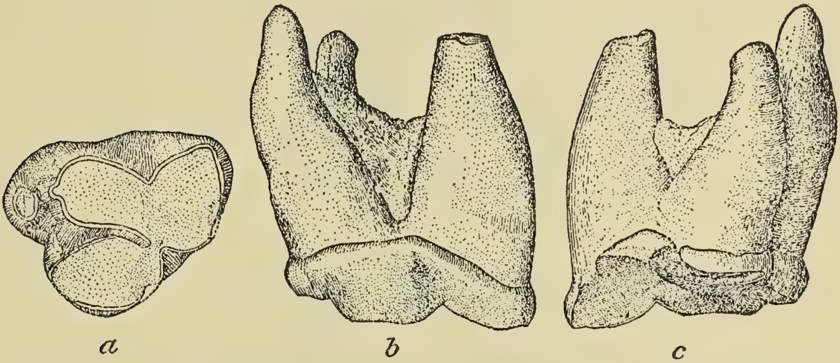


Fig. 13. *Indarctos* (?) *oregonensis* Merriam, Stock, and Moody. P$\underline{4}$, No. 22362 U.C.C.; *a*, occlusal view; *b*, outer view; *c*, inner view; ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

M$\underline{2}$ (fig. 14) of the bear from the Rattlesnake beds most nearly resembles that of the ursid type described by Pilgrim[15] from the middle or upper Siwalik beds of India under the name of *Indarctos salmontanus*. M$\underline{2}$ of No. 22362 resembles the type of *I. salmontanus* in its unusual relation of width to antero-posterior diameter, and in the stage of development of the heel. The antero-posterior and transverse diameters are almost identical with those of the type of *I. salmontanus*. As in the Indian species, the paracone and metacone of No. 22362 are clearly defined, the paracone being considerably larger than the metacone. In No. 22362, as in *I. salmon-*

[15] G. E. Pilgrim, Records, Geological Survey of India, vol. 44, pt. 3, pp. 225–233, pl. 20, 1914.

tanus, there is evidence of a large tubercle immediately behind the antero-internal ridge, corresponding evidently to the hypocone. The extreme posterior end of the heel consists of a transverse ridge which is largely worn down.

Considering that in No. 22362 M$\underline{2}$ is considerably worn, and allowing for individual variation, the resemblances between the Oregon specimen and the type of *I. salmontanus* are close. Small differences, such as the more distinctly circular cross-section of the metacone, the smaller hypocone, slightly longer heel, and wider trigon region in the Oregon form, suggest specific distinction such as would be expected in individuals so widely separated geographically.

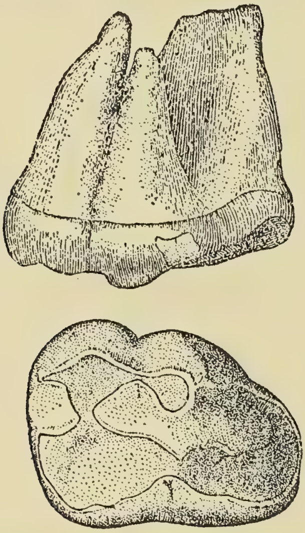


Fig. 14. *Indarctos* (?) *oregonensis* Merriam, Stock, and Moody. M$\underline{2}$, No. 22362 U.C.C.; occlusal and outer views. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

The characters of M$\underline{2}$ in the Oregon form and in *Indarctos salmontanus* approach those of *Hyaenarctos* except in relative elongation of the heel. The two outer cusps of M$\underline{2}$ in *Hyaenarctos* may show somewhat stronger lateral compression than is noted in the Oregon form. The antero-internal ridge in *Hyaenarctos* may apparently show almost no separation into two divisions, or may be very distinctly divided as in *H. palaeindicus*, in which the hypocone region is imperfectly developed. In *H. punjabiensis* an incipient heel is clearly shown, though it is much less pronounced than in *Indarctos*.

M$\underline{2}$ of the Rattlesnake specimen is distinguished from that of

Arctotherium by its greater width and much shorter talon. In *Arctotherium* the primitive quadritubercular portion of the tooth is longer antero-posteriorly and the heel is much longer. The arrangement of the tubercles is much the same in the two types, but the tubercles show stronger lateral compression in *Arctotherium.*

The arrangement of the roots supporting M$\underline{2}$ in the Oregon specimen differs somewhat from that in *Arctotherium simum.* In No. 22362 there are two distinct external roots supporting the paracone and metacone regions. These roots in both available teeth are distinct, but are not widely separated. The inner and posterior region is supported by a large, broad root evidently composed of two parts, one of which supports the protocone region and the other originates above the hypocone and the region behind it. In *Arctotherium* there are also evidently four original root elements, but the roots beneath the paracone and metacone tend to diverge widely, the element above the metacone being in some cases united with the posterior root supporting the heel. In *Arctotherium* the root supporting the protocone may or may not unite with the root above the heel.

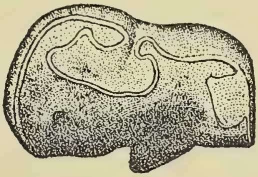


FIG. 15. *Indarctos* (?) *oregonensis* Merriam, Stock, and Moody. M$\bar{2}$, No. 22362 U.C.C.; occlusal view. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

M$\bar{2}$ (fig. 15) is distinguished from the corresponding element in the dentition of *Hyaenarctos* and of certain forms of *Arctotherium* by the relative proportions of the trigonid and talonid regions. In the Oregon specimen the antero-posterior diameter of trigonid and talonid are, as nearly as can be determined, approximately equal. The tuberculation of M$\bar{2}$ represents only the inner side of the tooth, on which is shown the relatively high region occupied by the metaconid, and the lower more or less basin-like talonid region. The talonid possessed a rather wide hypoconid ridge, and two smaller cusps on the inner border as in *Hyaenarctos.* The crown of M$\bar{2}$ is supported upon two roots, of which the posterior is the larger.

Skeletal elements.—Perhaps the most characteristic element of the

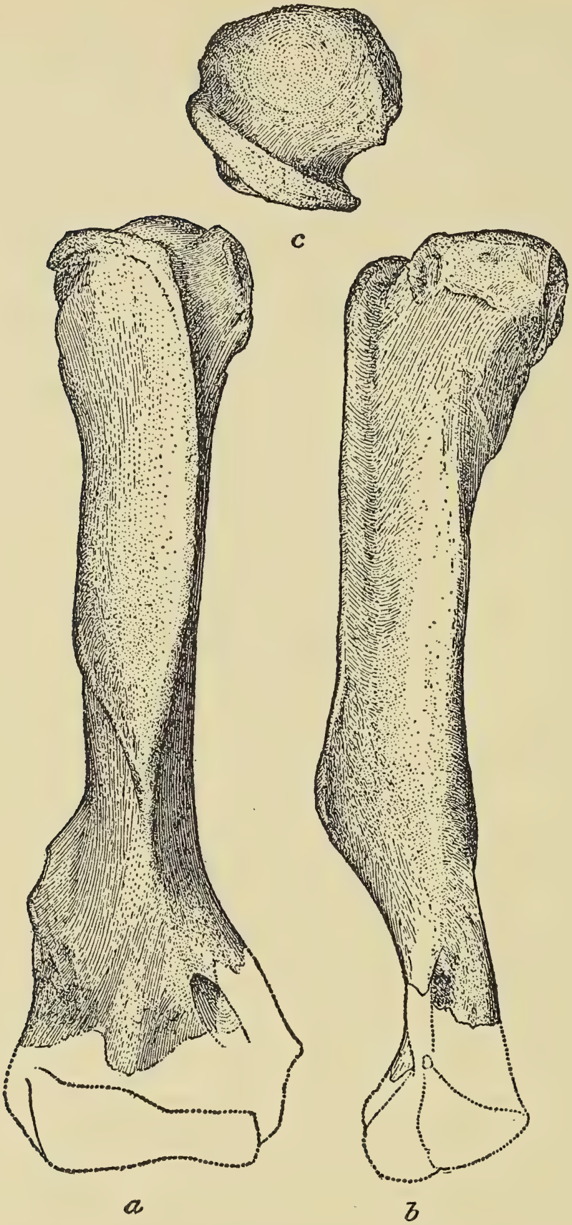


FIG. 16. *Indarctos* (?) *oregonensis* Merriam, Stock, and Moody. Humerus, No. 22362 U.C.C.; *a*, anterior view; *b*, inner view; *c*, proximal view. ×0.25. Rattlesnake Pliocene, John Day Valley, Oregon.

skeletal structures is the humerus (fig. 16). This specimen in No. 22362 is much more massive than the humerus of the California *Arctotherium*, and in this respect suggests the relatively heavy skeletal elements of *Hyaenarctos*. The humerus from the Rattlesnake beds resembles that of *Arctotherium* in the presence of an entepicondylar foramen.

The remaining skeletal elements belonging to No. 22362 from the Rattlesnake formation are, or tend to be, larger and heavier than the corresponding structures in *Arctotherium*.

Relationships.—The Oregon Pliocene bear approximates the characters of *Indarctos salmontanus* Pilgrim in the structure of M$\underline{2}$, the only available tooth representing that genus. The characters seen in the type of *Indarctos* and in the Oregon specimen are not found in other known forms. These characters are most nearly approached in M$\underline{2}$ of *Hyaenarctos*, *Arctotherium*, and *Aeluropus*, and are intermediate between those of *Hyaenarctos* and *Arctotherium*. In the characters of P$\underline{4}$ the Oregon specimen does not differ essentially from the several known species of *Hyaenarctos*, but is distinctly different from *Arctotherium*, *Aeluropus*, and all other known forms referred to the bear group.

The characters of the massive limb elements of the Oregon specimen suggest the limb type of *Hyaenarctos*, and indicate a rather wide separation from *Arctotherium*.

The sum of the known characters of the Oregon bear, specimen 22362, represent a type near *Hyaenarctos*, but tending toward *Arctotherium* in the development of its last upper molar. The *Indarctos* group is nearer to *Hyaenarctos* than to *Arctotherium* and, as suggested by Pilgrim,[16] the discovery of a type intermediate between *Hyaenarctos punjabiensis* and *Indarctos salmontanus* might make it difficult to establish a generic separation between *Indarctos* and *Hyaenarctos*.

Indarctos (?) sp.

A single upper carnassial, No. 22461 (fig. 17), from U.C.C. locality 3042, represents an ursid type, differing slightly from the type specimen of *Indarctos*(*?*) *oregonensis*. This specimen was found resting upon beds of the Mascall Miocene, but was immediately below an occurrence of Rattlesnake Pliocene. No. 22461 agrees with the carnassial of the type specimen of *I.* (*?*) *oregonensis* approximately in its proportions, but differs in the smaller size of the tooth as a whole and in the relatively smaller parastyle of No. 22461. A large part of the protocone is broken away, but the root and a portion of this tubercle remaining indicate that the protocone was of large size.

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[16] G. E. Pilgrim, Records, Geol. Surv. India, vol. 44, pt. 3, p. 227, 1914.

Measurements (in millimeters) of P$\underline{4}$, No. 22461, are as follows: antero-posterior diameter, 26.7; transverse diameter across protocone (approximately), 19; antero-posterior diameter of paracone at base, 13; antero-posterior diameter of paracone along median line, 3.7.

This specimen differs from P$\underline{4}$ of the type of *I.*(*?*) *oregonensis* essentially in the somewhat smaller size of the protocone and in the different form of the parastyle. Although the parastyle of No. 22461 has an antero-posterior diameter approximating that of the type specimen of *I.* (*?*) *oregonensis*, the parastyle in the latter is in reality heavier and probably of more distinctly conical form. Specimen 22461 presumably represents a different species and possibly a different genus from that of the type specimen of *I.* (*?*) *oregonensis*. It is tentatively to be referred to the Ursidae, and presumably represents either *Indarctos* or *Hyaenarctos*. A small portion of the maxillary in No. 22461 shows the alveolus of a P$\underline{3}$, which is distinctly two-rooted. In this respect No. 22461 resembles certain forms of *Arctotherium*. *Hyaenarctos sivalensis* seems also to possess a two-rooted P$\underline{3}$.

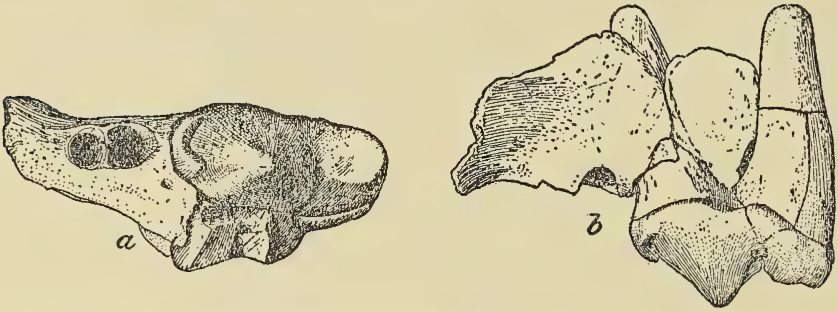


FIG. 17. *Indarctos* (?) sp. P$\underline{4}$, No. 22461 U.C.C.; *a*, occlusal view; *b*, outer view. ×1.0. Rattlesnake Pliocene, or Mascall Miocene, John Day Valley, Oregon.

P$\underline{3}$ of *Hemicyon sansaniensis* is a large tooth which seems to have possessed two roots although the writers have not been able to make certain of this character. In $P\underline{4}$ of *Hemicyon sansaniensis* the protocone is very large, and there is evidently an incipient parastyle developing upon the cingulum. The protocone is smaller than in No. 22461, and the parastyle is also smaller, but there is a very suggestive resemblance.

If No. 22461 is derived from the Mascall Miocene instead of from the Rattlesnake Pliocene its somewhat smaller size and slightly less specialized characters would probably be associated with other evidences of less-advanced stage of evolution than that of *Indarctos* (*?*) *oregonensis* of the Rattlesnake.

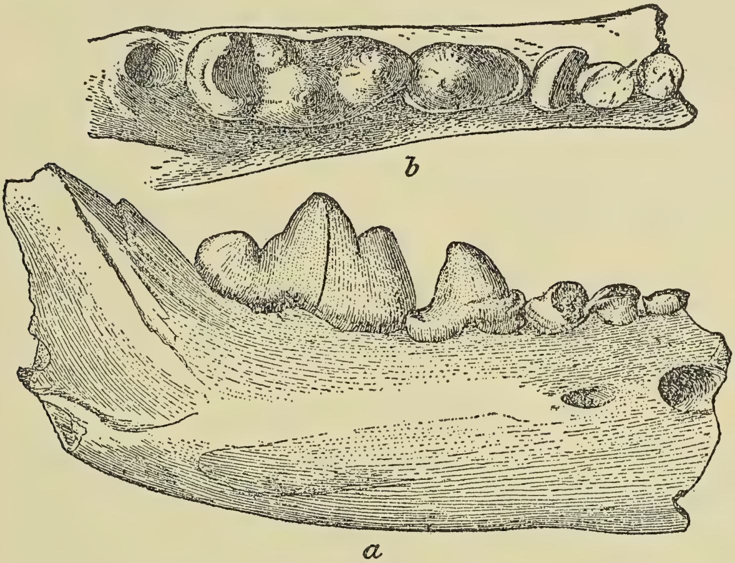


FIG. 18. *Mustela* n. sp. Fragmentary ramus of mandible with teeth, No. 22463 U.C.C.; *a*, outer view; *b*, occlusal view. ×2.0. Rattlesnake Pliocene, John Day Valley, Oregon.

Mustela n. sp.

Lower jaw, No. 22463 (fig. 18), from U. C. locality 3045 in the Rattlesnake formation, represents a *Mustela* different from any previously described from the Pliocene deposits of the Great Basin region. This specimen consists of a portion of the right ramus of the mandible with $P\overline{4}$, $M\overline{1}$, the alveoli of the canine, with parts of $P\overline{2}$, $P\overline{3}$, and $M\overline{2}$. The first lower molar is of typical musteline form with a short wide heel on which the hypoconid is a well-developed ridge connecting with the lower eminence of the postero-internal region of the heel. The shearing blade is well developed. The metaconid is large.

The alveolus of M2̄ represents the insertion of a single large root. P4̄ has a well-developed heel, the posterior region of the protoconid is slightly worn, but the posterior cusp seems not to have been present. P3̄ was two-rooted. The portion of the mandible available has dimensions twice those of the pine marten. Two mental foramina are present; one is situated near a point below the root of P2̄, and the other below the posterior root of P3̄.

A second small fragment of a musteline jaw, No. 22464 (fig. 19), represents a species but little more than half the size of that known by No. 22463. There is present only the worn posterior half of M1̄ and the crown of M2̄. This species is distinct from that represented by No. 22463.

Measurements (in Millimeters) of Lower Jaw, No. 22463

Length of tooth series, P2̄ to M2̄ inclusive, alveolar measurement	34.4
P4̄, antero-posterior diameter	8.1
P4̄, greatest transverse diameter	4.3
M1̄, antero-posterior diameter	13.8
M1̄, greatest transverse diameter	5.6
M1̄, transverse diameter of heel	5.2
Depth of mandible below anterior end of M1̄	12
Thickness of mandible below middle of M1̄	6.7

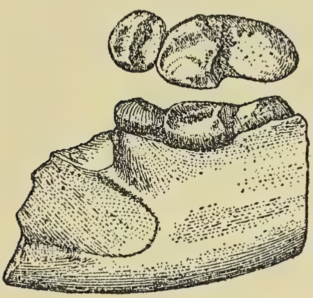
Felid sp. A, large

A distal end of a humerus, No. 309, fig. 20, belonging to a felid form is slightly smaller than the corresponding part in *Smilodon*. In the Rattlesnake specimen the position of the entepicondyler foramen resembles that in the humerus of the lion more than that of the saber-tooth. The opening in *Smilodon* extends farther internally, reaching slightly beyond a vertical line drawn from the inner end of the distal trochlea and parallel to the main axis of the shaft. In *Felis* the foramen does not tend to reach beyond such a line. The Rattlesnake specimen resembles the true cats in this character.

Two specimens, a scaphoid-lunar and a phalangeal element (figs. 21 and 22), collected at U. C. locality 3060, are comparable in size to corresponding structures in *Smilodon*. The material may represent the same type of cat as that known by the fragment of the humerus, or may belong to a species or genus distinct from the latter.

Felid sp. B, small

A distal end of a humerus, No. 23859, found at U. C. locality 3058, pertains to a cat much smaller than that represented by specimen 309 described above. It belongs to a form smaller than either *Felis daggetti* from the Pleistocene of Rancho La Brea or the Recent mountain lion of California.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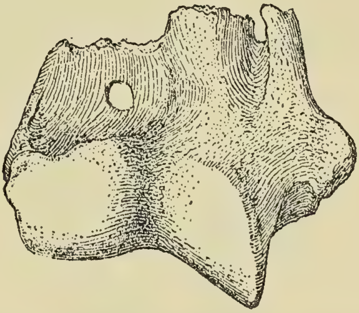
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Fig. 19. Musteline jaw fragment, No. 22464 U.C.C.; lateral and occlusal views. ×2.0. Rattlesnake Pliocene, John Day Valley, Oregon.

Fig. 20. Felid sp. *A*, large. Distal end of humerus, No. 309 U.C.C.; anterior view. ×0.50. Rattlesnake Pliocene, John Day Valley, Oregon.

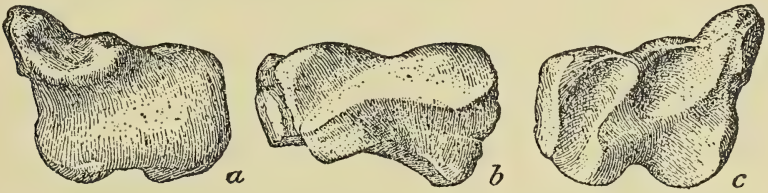


Fig. 21. Felid sp. Scaphoid-lunar, No. 26786 U.C.C.; *a*, proximal view; *b*, anterior view; *c*, distal view. ×0.50. Rattlesnake Pliocene, John Day Valley, Oregon.

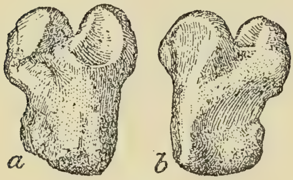
RODENTIA

A fragmentary ramus of the mandible, No. 26793, from University of California locality 3058, fig. 23, represents a squirrel type in the Rattlesnake fauna. The specimen was submitted to Dr. J. W. Gidley of the U. S. National Museum. Dr. Gidley has kindly furnished a description of the material and has concluded that it undoubtedly represents a new specific form. This statement is given below.

We take pleasure in naming the species for Dr. Gidley.

Otospermophilus gidleyi n. sp.

This specimen from the Oregon Pliocene seems to represent a true *Citellus* in the broader meaning of the genus name. *Citellus*, however, has been split up into several genera or subgenera the characters of which are based mainly on skull modifications, and whose relative value is a matter of opinion. With only the material in hand, therefore, there is some uncertainty regarding the exact position of the Pliocene species in reference to these minor groups.



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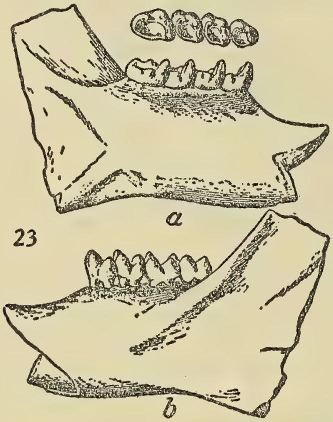

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FIG. 22. Felid sp. Phalangeal element, No. 26787 U.C.C.; *a*, dorsal view; *b*, ventral view. ×0.50. Rattlesnake Pliocene, John Day Valley, Oregon.

FIG. 23. *Otospermophilus gidleyi*, n. sp. Ramus of mandible, No. 26793 U.C.C.; *a*, inner view with occlusal view of teeth; *b*, outer view. ×2.0. Rattlesnake Pliocene, John Day Valley, Oregon.

It is clearly distinguished from the other sciurids by the combined characters of the relatively shorter anteroposterior extent of all the cheek teeth.

The dental characters are very similar to those of *Otospermophilus*, the group to which I would tentatively refer it. In common with the species of this group the cheek teeth are low crowned, with relatively little heightening of the trigonid portions, and in P$\overline{4}$ the two subequal cusps of the trigonid are closely appressed, making this tooth nearly triangular in outline. These characters are in contrast with the more highly specialized cheek teeth of true *Citellus*, in which the trigonid ridge of P$\overline{4}$ is widened almost as much as in the molars through the wider separation of these cusps, and this portion of all the molars is relatively much heightened. Comparing the fossil species with *O. adocetus* (No. 126120 U. S. Nat. Mus., Biol. Sur. Coll.), a species now living in Mexico, with which it agrees very nearly in size, and with the California species, *O. beecheyi* (No. 3559, U. S. Nat. Mus., Biol. Sur. Coll.), about the only differences to be noted are as follows: In the fossil the talonid basins of all the lower cheek teeth are relatively somewhat shallower and definitely broader in area, the main outer cusps (protoconid and hypoconid) being slightly more marginal in position. The entoconids are almost completely obscured in the nearly continuous, relatively low, and evenly curved postero-internal rim of the talonid basins as in *O. beecheyi*. But the talonid rim is somewhat less elevated and the notch between the rim and the paraconid is less pronounced, being partially filled by a small intermediary cusp not observed or but rarely found in the living species. In *Citellus* and other sciurids in general this border is more or less angulate, and usually the entoconid, though small, is rather clearly defined. A character which seems to distinguish the fossil distinctly from the living species of the citellid group is the much greater relative depth and apparently shorter proportions of the lower jaw. This character and the more marginal position of the outer cusps are common to species of the more generalized types, and seem to indicate a somewhat less progressive stage of development of the fossil species as compared with the living citellids, although in some other respects it may be considered even more progressive than the living species, all of which suggest that the skull when known may present characters which would necessitate proposing a new subgroup for its reception. This step, in my opinion, however, is not warranted on what is presented in the type specimen.

LAGOMORPHA

Hypolagus, near vetus (Kellogg)

The rabbit remains from the Rattlesnake beds consist mainly of separate teeth and fragmentary limb elements. $P\overline{3}$ in the Oregon form resembles closely the corresponding tooth in the specimen from the Thousand Creek Pliocene referred to *Hypolagus vetus* by Dice.[17]

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[17] L. R. Dice, Systematic position of several American Tertiary Lagomorphs, Univ. Calif. Publ., Bull. Dept. Geol., vol. 10, pp. 181–182, 1917.

No. 23174 (fig. 24) is slightly smaller than $P\overline{3}$ in the Thousand Creek specimen and the anterior re-entrant angle is a trifle deeper in the former tooth. On the whole, the enamel pattern in the tooth from the Rattlesnake approximates closely that in No. 12567 from Nevada.

A number of upper cheek-teeth are preserved, one of which resembles very closely in size and shape No. 19799 from the Cedar Mountain beds, Stewart Valley Miocene of Nevada.

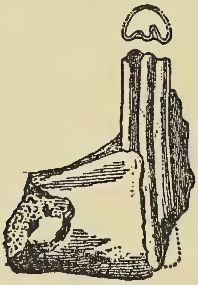

Fig. 24. *Hypolagus*, near *vetus* (Kellogg). Mandibular fragment with $P\overline{3}$, No. 23174 U.C.C.; lateral view with view of occlusal surface of tooth. ×2.0. Rattlesnake Pliocene, John Day Valley, Oregon.

EDENTATA

Megalonychid? gen. and sp. indet.

A single, fragmentary metapodial, No. 22900 (fig. 25), was collected at U. C. locality 3061 in the Rattlesnake beds. This specimen has been described by Stock,[18] and the following description and comparison can be quoted as follows:

"No. 22900 is short and stout. The lateral wall of the shaft is at right angles to that portion of the dorsal surface which still remains. It indicates that the metapodial possessed a relatively deep shaft and that the latter was presumably quadrilateral in section. The lateral facet for adjoining metapodial is flat and oval and is directed outward and downward. The proximal margin of this facet is not closely approached by the mesopodial surface, but this may be due in part to the worn condition of the specimen. The remaining portion of the mesopodial surface is but slightly concave transversely and does not reach the dorsal margin of the proximal end. Although an offset flanks the lower portion of the distal carina on one side, there was apparently not an extensive offset present on the opposite side.

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[18] C. Stock, Carnegie Inst. Wash. Pub. No. 331, pp. 20–22, 1925.

"The Rattlesnake specimen resembles the third metacarpal of *Hapalops* in quadrilateral cross-section of shaft. It differs, however, from this element in having a relatively shorter and deeper shaft. In *Hapalops* the proximal facet of the inner side is more extensive dorso-ventrally, is directed for the most part proximo-internally, and is of an entirely different shape than in No. 22900. The dorsal margin of the proximal end in the latter specimen was not deeply indented in middle line as in the Miocene form. The distal carina in *Hapalops* is slightly more prominent dorsally and the inner offset is also more extensive above than is the offset preserved in the Pliocene metapodial.

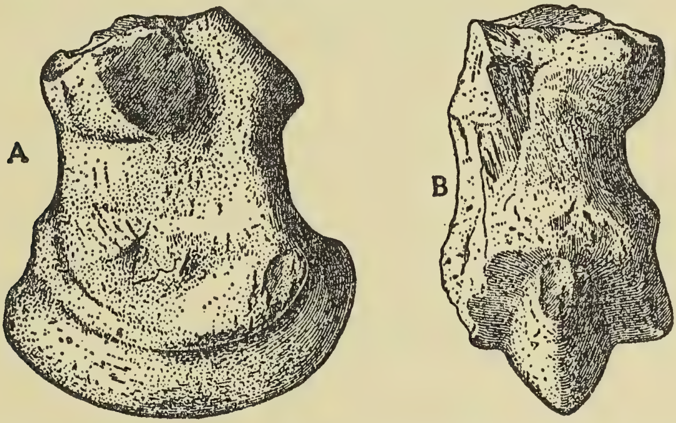

Fig. 25. Megalonychid? gen. and sp. indet. Metapodial, No. 22900 U.C.C.; *A*, side view; *B*, dorsal view. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

"Metacarpal III of *Megalonyx jeffersonii* is approximately twice as long as No. 22900 from the Pliocene. The shaft in the Pleistocene genus is relatively shorter than in *Hapalops*, but not as short as in the Rattlesnake specimen.

"With metatarsal II of *H. elongatus* certain differences and resemblances are to be noted. No. 22900 is relatively shorter and the shaft deeper; the later facet is small and flattened, while in *Hapalops* the facet for metatarsal I is relatively large and concave dorso-ventrally; the offset, which is preserved at the distal end, is less extensively developed. In the metatarsal of *Hapalops* (No. 15545

Princeton Univ. Coll.) under observation, the lateral facet articulating with the first metapodial has much the same position and is directed downward in much the same manner as the facet in No. 22900. Below this facet in the Rattlesnake specimen there is some indication of a small knob or boss, as in the second metatarsal from the Santa Cruz beds. Dr. W. J. Sinclair, who has kindly examined a plaster cast of the Rattlesnake specimen, is of the opinion that it represents a second metatarsal and refers it to the right pes. He remarks that the proximal surface is flatter than in *Hapalops*, and in metatarsal II of the latter genus and of *Analcimorphus* this facet and the anterior (dorsal) surface meet in a markedly concave margin, which is not the case in the Pliocene form. If the specimen does represent the second metatarsal, then the inner facet is for the first metatarsal and the proximal surface for the mesocuneiform, as stated by Dr. Sinclair."

COMPARATIVE MEASUREMENTS (IN MILLIMETERS)

	Length through middle.	Depth of distal carina.	Least depth of shaft.
No. 22900, Rattlesnake	*52	46.8	30.3
Hapalops elongatus, metatarsal II, No. 15545, Santa Cruz	20.6	16.2	7.6
Analcimorphus sp.,† metatarsal II, Santa Cruz	30.3	7.6	15

* Approximate.

† Measurements taken by W. J. Sinclair.

PROBOSCIDEA

Proboscidean Remains

A number of fragments of cheek-teeth of mastodontine forms are known from the Rattlesnake, but as yet no specimens have been found which show characters sufficiently expressed to permit identification.

EQUIDAE

Pliohippus spectans (Cope)

The type specimen of *Pliohippus spectans* described by Cope[19] consists of two upper cheek-teeth[20] listed from Cottonwood, Oregon, the type locality of both Mascall and Rattlesnake formations. The teeth came from a dirty grayish to reddish matrix having a closer resemblance to the characteristic Rattlesnake beds than to the Mascall. The well-authenticated occurrence of *Pliohippus* in place in the Rattlesnake formation and its absence from the Mascall collections taken with the suggested nature of the matrix on the type of *P. spectans* furnish almost conclusive evidence that this species is a Rattlesnake and not a Mascall form.

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[19] E. D. Cope, Amer. Nat., vol. 14, p. 223, 1880.

[20] For figures of these teeth see H. F. Osborn, Mem. Amer. Mus. Nat. Hist., n.s., vol. 2, pt. 1, p. 165, fig. 132, 1918.

The species as described by Cope was characterized as possessing very wide fossettes with simple enamel borders, narrow crescents, and small columns. As has already been noted by other writers, this species is a typical member of the *Pliohippus* group as now defined. Its stage of development is near that of *P. interpolatus* of the Clarendon of Texas or of *P. fairbanksi* from the Ricardo Pliocene of the Mohave Desert.

A *Pliohippus* specimen, No. 22388 (fig. 26), from U. C. locality 3060 in the Rattlesnake, is evidently to be referred to *Pliohippus spectans*. No. 22388 includes a complete upper and lower cheek-tooth series. The large crowns of the upper teeth are heavily cemented and moderately curved. The fossettes are wide and show little crinkling of their enamel walls. The protocone of the premolars is very small, is nearly circular in cross-section, and is set off from the protoconule by a sharp notch on the anterior side of the protoloph. In the posterior molars the protocone is somewhat flattened and curved backward toward the hypocone. The characters of the protocone of the premolars resemble those in *P. interpolatus* and *P. fairbanksi*, but the sum of the characters of $M\underline{1}$ and $M\underline{2}$ is closely similar to that in the type molar tooth of *P. spectans*. The species as represented by the present material shows resemblance to *P. interpolatus* but is somewhat smaller. Unfortunately material is not available for comparison with the posterior cheek-teeth of that species. *P. fairbanksi* of the Ricardo Pliocene is also a similar form though distinguished by narrower fossettes. Unfortunately the posterior cheek-teeth of *P. fairbanksi* have not yet been described.

A large functional $P\underline{1}$ is present in the dentition of No. 22388.

The lower cheek-tooth series of *P. spectans* as represented in No. 22388 (fig. 26*c*) shows the premolars much wider and heavier than the molars, the difference between the occlusal areas of premolar and molar regions being very marked. The metaconid-metastylid column is short and the inner groove narrow. In the molars the parastylid extends toward the median side as far as the inner border of the metaconid-metastylid column, but in the premolars it falls short of reaching this plane. The antero-internal angle of the entoconid approaches a right angle. The outer walls of protoconid and hypoconid are strongly convex.

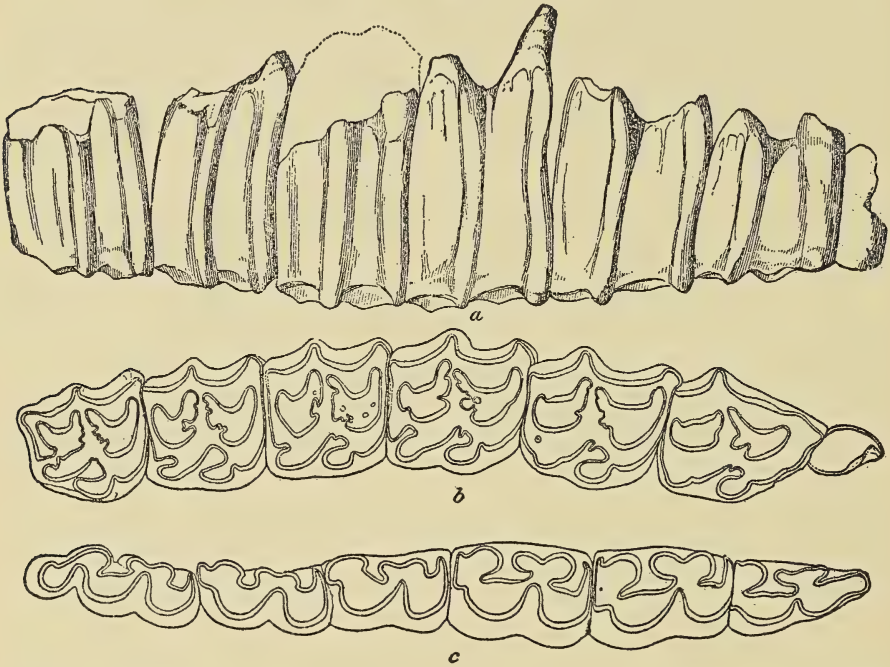

Fig. 26. *Pliohippus spectans* (Cope). Superior and inferior cheek-teeth, No. 22388 U.C.C.; *a*, outer view, P$\underline{1}$ to M$\underline{3}$ inclusive; *b*, occlusal view, P$\underline{1}$ to M$\underline{3}$ inclusive; *c*, occlusal view, P$\bar{2}$ to M$\bar{3}$ inclusive. × 0.6 (approximate). Rattlesnake Pliocene, John Day Valley, Oregon.

A series of somewhat worn cheek-teeth (fig. 27), representing *Pliohippus*, show characters near those of No. 22388 and presumably belong to *P. spectans*. In No. 22391 the crowns are slightly smaller than in No. 22388, and show a slightly greater wear. In this specimen the protocone is united posteriorly with the hypocone. This character may be diagnostic of a group distinct from that represented by No. 22388 or it may be due merely to advanced wear.

A number of scattered incisor teeth found with *Pliohippus* specimens show large crowns with deep cement-filled pits. These teeth are presumably in some part to be referred to *P. spectans.*

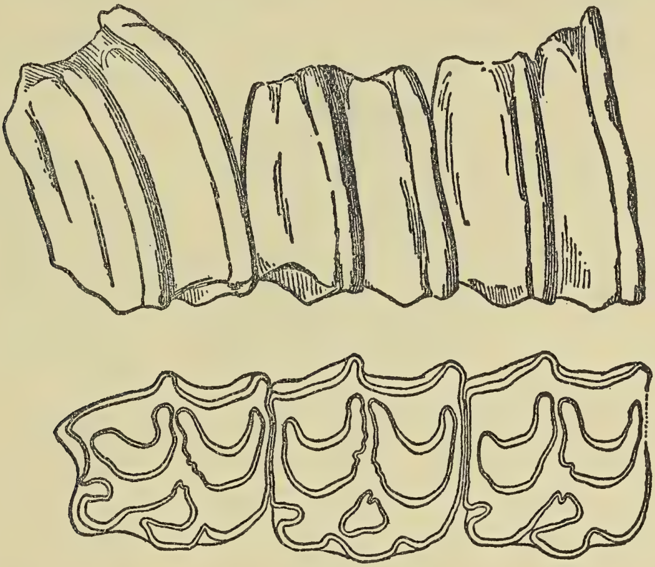

FIG. 27. *Pliohippus spectans* (Cope). Superior cheek-teeth, No. 22391 U.C.C.; outer and occlusal views. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

MEASUREMENTS (IN MILLIMETERS) OF DENTITION, No. 22388

Length of tooth-row from anterior end of P$\underline{1}$ to posterior end of M$\underline{3}$	173.8	Length of tooth-row from anterior end of P$\overline{2}$ to posterior end of M$\overline{3}$	165.1
P$\underline{1}$, antero-posterior diameter	14.5	P$\overline{2}$, antero-posterior diameter	29
P$\underline{1}$, transverse diameter	9.4	P$\overline{2}$, transverse diameter	13
P$\underline{2}$, antero-posterior diameter	31.5	P$\overline{3}$, antero-posterior diameter	27.4
P$\underline{2}$, transverse diameter	24	P$\overline{3}$, transverse diameter	15.5
P$\underline{3}$, antero-posterior diameter	29.2	P$\overline{4}$, antero-posterior diameter	28.4
P$\underline{3}$, transverse diameter	26.2	P$\overline{4}$, transverse diameter	14
P$\underline{4}$, antero-posterior diameter	29.2	M$\overline{1}$, antero-posterior diameter	24.7
P$\underline{4}$, transverse diameter	26.5	M$\overline{1}$, transverse diameter	12.5
M$\underline{1}$, antero-posterior diameter	26	M$\overline{2}$, antero-posterior diameter	26.2
M$\underline{1}$, transverse diameter	26.8	M$\overline{2}$, transverse diameter	11.4
M$\underline{2}$, antero-posterior diameter	25.3	M$\overline{3}$, antero-posterior diameter	31.7
M$\underline{2}$, transverse diameter	24.6	M$\overline{3}$, transverse diameter	10
M$\underline{3}$, antero-posterior diameter	27.2		
M$\underline{3}$, transverse diameter	22		

Milk Dentition of Pliohippus

Several upper milk teeth of *Pliohippus* (fig. 28), from the Rattlesnake beds have heavily cemented subhypsodont crowns. The enamel bordering the fossettes shows only moderate folding. The protocone is small and flattened or crescent-shaped in the little-worn teeth. In a worn Dm$\underline{3}$, No. 2193 (fig. 28*a*), the protocone is nearly circular in cross-section. These teeth are larger than any milk teeth of the *Pliohippus* type known thus far from the Ricardo Pliocene.

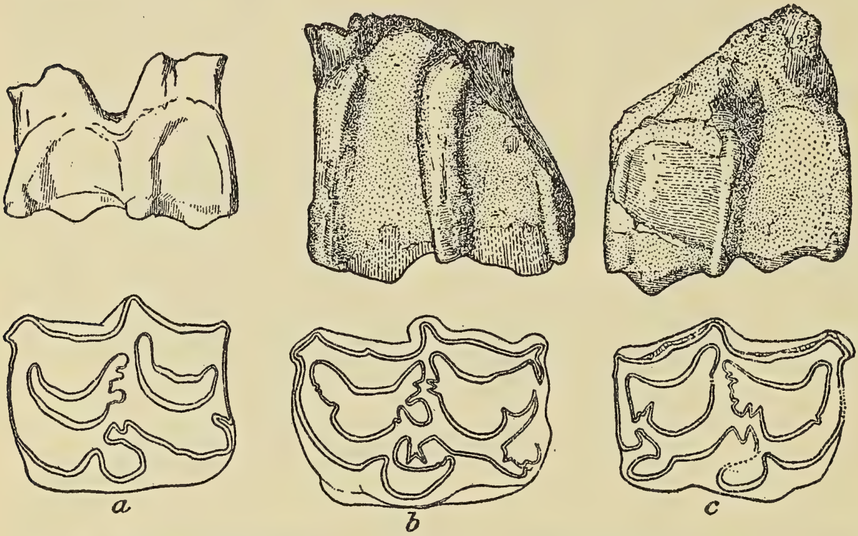

Fig. 28. *Pliohippus*, probably *spectans* (Cope). Superior deciduous cheek-teeth, lateral and occlusal views; *a*, Dm$\underline{3}$, No. 2193 U.C.C.; *b*, No. 26791 U.C.C.; *c*, No. 22392 U.C.C. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

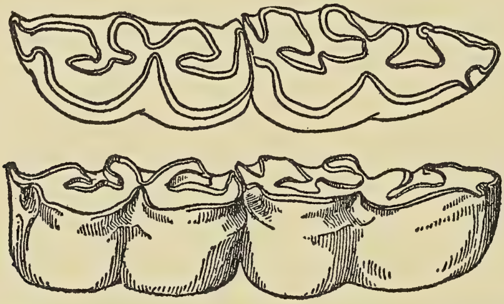

Fig. 29. *Pliohippus*, probably *spectans* (Cope). Dm$\bar{2}$ and Dm$\bar{3}$, No. 22393 U.C.C.; occlusal and outer views. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

The lower cheek-teeth of the milk dentition of *Pliohippus* forms from the Rattlesnake are represented in several specimens. These teeth are heavily cemented and short-hypsodont. The metaconid-metastylid column is narrower transversely, and its inner groove somewhat wider than in the permanent premolars of forms known from this horizon. In Dm$\overline{2}$ the entoconid is often truncated obliquely at the anterior end more as in *Merychippus* than is the case in permanent P$\overline{2}$ of this species. As shown in No. 22393 (fig. 29), Dm$\overline{2}$ may have an antero-external fold on the parastylid and a small fold on the inner side of the hypoconid.

Measurements (in Millimeters) of Milk Dentition, No. 22395

Dm$\overline{2}$, antero-posterior diameter	34.1	Dm$\overline{3}$, greatest transverse diameter	13.3
Dm$\overline{2}$, greatest transverse diameter	12.7	Dm$\overline{4}$, antero-posterior diameter	32.7
Dm$\overline{3}$, antero-posterior diameter	30.8	Dm$\overline{4}$, greatest transverse diameter	12.6

Equid Limb Elements

An anterior and a posterior equid metapodial from the Rattlesnake represent horses having approximately the size of the larger horses of the Ricardo Pliocene. Metatarsal III (fig. 31*c*) was secured at locality 3060 in association with the cheek-teeth of *Pliohippus spectans*, and the metapodial belongs presumably to this species. On both the front and hind metapodials the distal keel is strongly developed on the anterior side of the distal articular face. The shaft is much less slender than in *Hipparion whitneyi* and approaches rather the proportions in *Pliohippus*. The facets of the proximal end are not shown.

Measurements (in Millimeters) of Metapodials

	Metacarpal III No. 2230.	Metatarsal III No. 22425.
Greatest length (approximate)	196.8	238.5
Width of shaft immediately below middle	28	25.1
Greatest antero-posterior diameter of shaft at middle	20.3	25.2
Width of distal articulating surface (approximate)	34.6	37.1

Hipparion sinclairi (Wortman)

The type of this species was described from Cottonwood Creek in the John Day region of Oregon. The original specimen was obtained within the limits of the typical area of the Mascall Miocene and of the Rattlesnake Pliocene, and was found in the loose gravels above the Mascall. There is therefore good reason for considering the occurrence of this species as in the Rattlesnake formation.

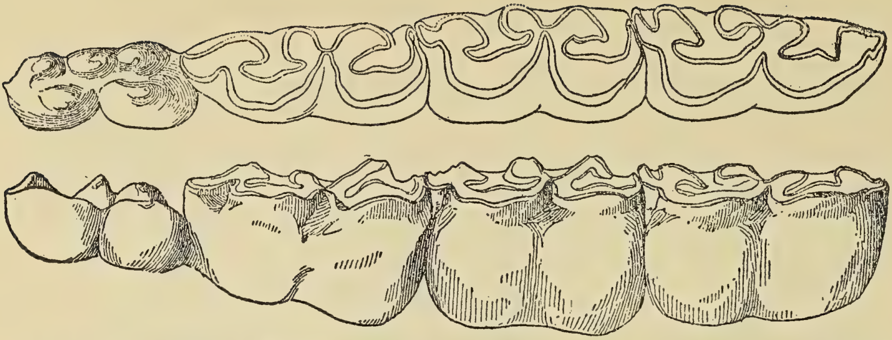

FIG. 30. *Pliohippus,* probably *spectans* (Cope). Dm$\bar{2}$, Dm$\bar{3}$, Dm$\bar{4}$, and M$\bar{1}$, No. 22395 U.C.C.; occlusal and outer views. ×0.95. Rattlesnake Pliocene, John Day Valley, Oregon.

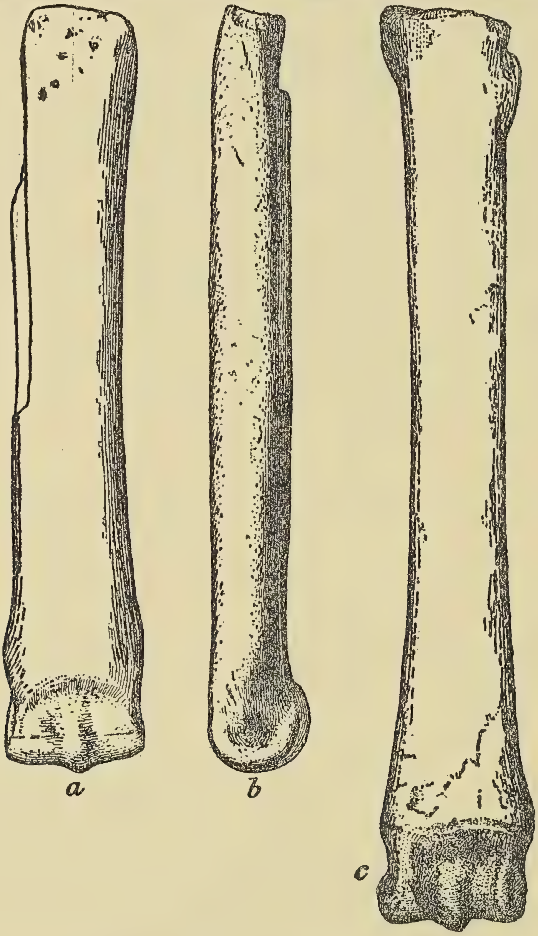

FIG. 31. Equid limb elements. Metacarpal III, No. 2230 U.C.C.; *a*, anterior view; *b*, side view; *c*, metatarsal III, No. 22425 U.C.C., anterior view. ×0.50. Rattlesnake Pliocene, John Day Valley, Oregon.

The type specimen described by Wortman[21] is an upper cheek-tooth, possibly P$\underline{4}$, No. 8178 Amer. Mus. Coll. The species is described as showing characters in general similar to those of *Hipparion occidentale*, but separated from that form by smaller size and "less marked concavity of the antero-internal lobe."

Gidley[22] called attention to the fact that *H. sinclairi* is larger than *H. montezumae* and differs from that species in its relatively larger and differently formed protocone, and more simple enamel plications. Gidley also noted that the protocone is concave on the inner face as in *H. affine*.

An upper cheek-tooth (M$\underline{1}$?), No. 22363 (fig. 32*a*), from U. C. locality 3068 in the Rattlesnake beds corresponds approximately in form and dimensions to the type of *H. sinclairi*, and evidently represents that species. This tooth has dimensions of the crown near those of *Hipparion gratum*, but it differs from that species in the much greater antero-posterior diameter and lateral compression of the protocone. In the character of the protocone it resembles *Hipparion molle* from the Jacalitos portion of the Etchegoin Pliocene on the western border of the San Joaquin Valley, and *H. montezumae* from the later Tertiary beds of Lacualtipan, Hidalgo, Mexico. The Rattlesnake specimen is, however, considerably wider transversely than the known material of *H. molle*. The protocone of the type of *H. montezumae* is shorter antero-posteriorly than in No. 22363 and the fossettes seem narrower.

Specimen 22363 resembles *H. sinclairi* in the character of the fossettes and in the extreme compression of the protocone. The protocone is, however, more strongly compressed in No. 22363.

COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH

	Hipparion sinclairi, type P$\underline{4}$?	Hipparion sinclairi No. 22363 M$\underline{1}$?	Hipparion molle, type M$\underline{3}$.
Antero-posterior diameter	20.3	20	*a*19.3
Transverse diameter	19	20	*a*15.8
Antero-posterior diameter of protocone	8.7	9.9	9.4
Height of crown	42.3	....	48

a Approximate.

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[21] For figures of this specimen see H. F. Osborn, Mem. Amer. Mus. Nat. Hist., n.s., vol. 2, pt. 1, p. 196, fig. 159, 1918.

J. L. Wortman, Kansas City Rev. Sci. and Industry, vol. 6, No. 2, p. 73, 1882.

[22] J. W. Gidley, Bull. Amer. Mus. Nat. Hist., vol. 23, p. 900, 1907.

As the only material certainly determined as *H. molle* consists of three upper molars it is possible that additional collections will show a closer connection between *H. sinclairi*, *H. montezumae*, and *H. molle*. Whether or not these forms represent the same species it is worthy of note that they all seem to occur at a horizon near early Pliocene.

Two small lower cheek-teeth, No. 22381 (fig. 32*b*) and No. 22382, were associated with the upper tooth referred to *Hipparion sinclairi*. These specimens have dimensions such as might be expected in lower teeth of *H. sinclairi*. They are much smaller than a number of lower cheek-teeth which approximate the size of *H. occidentale*, and are evidently specifically distinct from the larger form. There seems good ground for determination of these specimens as *H. sinclairi*, of which the lower teeth have not been known up to this time. The two lower teeth referred to *H. sinclairi* are of closely comparable dimensions and are almost identical in form. They resemble the posterior premolars of certain of the more advanced protohippine horses in the extent to which the inner border of the metastylid projects beyond the entoconid on the median side, but the backward curvature of the crowns suggests a molar tooth. As

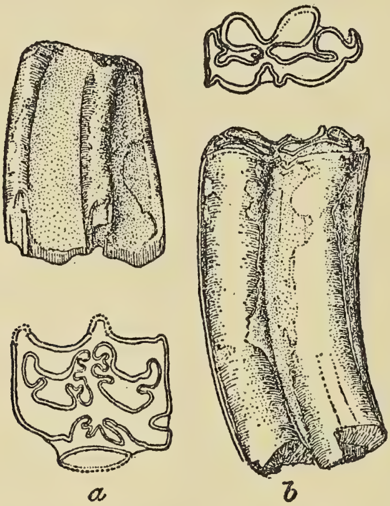

Fig. 32. *Hipparion sinclairi* (Wortman). Upper and lower cheek-teeth; *a*, M$\underline{1}$? No. 22363 U.C.C.; outer and occlusal views; *b*, lower molar, No. 22381 U.C.C.; outer and occlusal views. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

is indicated in figure 32*b*, the metaconid-metastylid column is long antero-posteriorly, and the valleys anterior and posterior to this column are very narrow. The antero-internal side of the entoconid is filled out and not obliquely truncated as in *Merychippus*. There is an antero-external ridge on the protoconid and a small but well-developed fold appears also on the antero-external wall of the hypoconid.

Measurements (in Millimeters) of Lower Teeth

	No. 22381.	No. 22382.
Antero-posterior diameter	21	21.8
Transverse diameter	10.2	10
Antero-posterior diameter of metaconid-metastylid column	13.1	14.1

Hipparion occidentale Leidy

This species is reported from beds in the John Day Valley in eastern Oregon by W. D. Matthew.[23] According to J. L. Wortman, the specimens reported by Matthew were collected from the Rattlesnake beds overlying the Mascall at Cottonwood Creek in the John Day Valley.

Two upper cheek-teeth, No. 26788 and No. 26789 (figs. 33, *a* and *b*), obtained at U. C. locality 3057, represent a *Hipparion* species larger than *H. sinclairi* and having a much smaller protocone. In many characters these teeth closely approach *Hipparion mohavense* of the Ricardo Pliocene. There is, however, a tendency to flattening of the protocone beyond the normal stage seen in the Ricardo species. The Rattlesnake species seems also to show a slightly stronger mesostyle and somewhat different folds in the enamel surrounding the fossettes. The characters of these Rattlesnake specimens seem well within the range of variation of *Hipparion occidentale* as at present known, and the writers hesitate to separate them from the Great Plains species.

A single cheek-tooth, No. 957 (fig. 33*c*), collected in the John Day region by a University of California party in 1900, shows characters near those of *Hipparion occidentale*. This specimen was found at locality 887, which was considered in the field to represent mainly Rattlesnake Pliocene. In the area in which collections were made at this locality Rattlesnake beds cap hills which are formed in part of Mascall Miocene. As yet no specimen of this nature is certainly known from the Mascall exposures. No. 957 approaches one form of *Hipparion occidentale* in size, in form of protocone, and in complication of the enamel bordering the posterior ends of the fossettes. The anterior border of the prefossette is without folds in No. 957, and the general appearance of the borders of the fossettes is one of relative simplicity. This tooth resembles *H. sinclairi* to some extent in the tendency toward simplicity of the enamel folds and in the form of the protocone, but the differences in pattern are considerable. *H. sinclairi* also differs from No. 957 in its considerably smaller size. It is possible that more material will show that the form of tooth seen in No. 957 grades into that of typical *H. sinclairi*. With existing material it appears to represent a distinct and larger species resembling in many respects one form of the Great Plains *H. occidentale*.

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[23] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 12, p. 70, 1899.

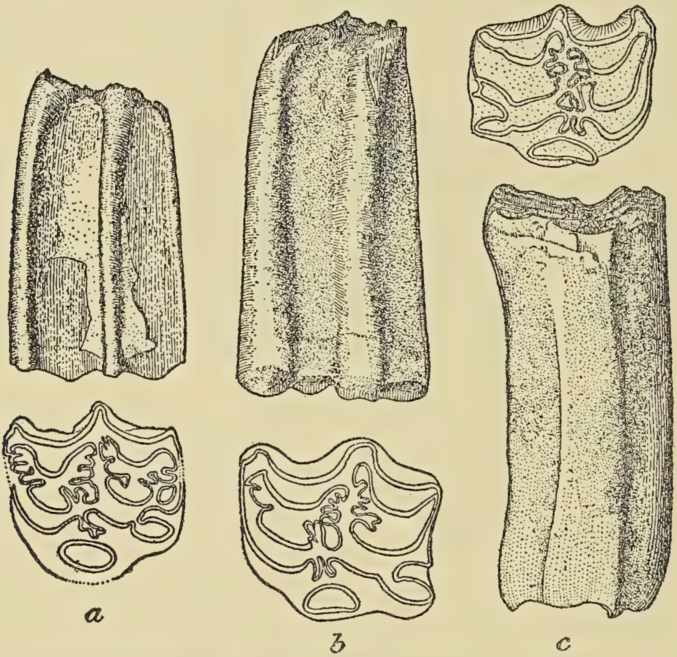

FIG. 33. *Hipparion occidentale* Leidy. Upper cheek-teeth; *a*, No. 26788 U.C.C., lateral and occlusal views; *b*, No. 26789 U.C.C., lateral and occlusal views; *c*, No. 957 U.C.C., inner and occlusal views. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF TEETH

	No. 957.	Hipparion occidentale, type.	Hipparion sinclairi, type.	Hipparion sinclairi, No. 22363 M1?
M2, antero-posterior diameter	23.5	23	20.3	20
M2, transverse diameter	20.1	22	19	20
M2, antero-posterior diameter of protocone	8.8	..	8.7	9.9
M2, height of crown	56.2	..	42.3	....

Hipparion leptode Merriam or Hipparion occidentale Leidy

Specimen No. 544 (fig. 34), consisting of three lower cheek-teeth of a large *Hipparion*, was collected by the 1900 party at locality 884 in the region of Rattlesnake Creek west of the Mascall ranch near Dayville, Oregon. These teeth came from an area in which both Rattlesnake and Mascall beds were exposed, but the reddish matrix showing in places on the teeth indicates quite certainly their derivation from the reddish or brownish tuffs of the Rattlesnake which here rests upon the white Mascall strata.

M2 of the Rattlesnake specimen (No. 544) resembles the peculiar *Hipparion leptode* from Thousand Creek in many characters. An antero-external ridge is present and strongly developed on the protoconid and the hypoconid in both forms. The metaconid-metastylid column is long and deeply grooved externally in both. The external groove is somewhat more acute at the inner end in the Rattlesnake specimen, but this may be due to difference in wear. The Rattlesnake specimen is somewhat shorter antero-posteriorly, and is a little less compressed laterally than the Thousand Creek type.

P2 and M1 of No. 544 resemble M2 in the presence of the strong antero-external ridge on the hypoconid. P2 and M1 differ from the Ricardo forms in the strength of the ridge on the hypoconid. The ridge may be present in the Ricardo specimens, but is very much weaker. In M1 the metaconid-metastylid column seems to show slightly more compression in the Rattlesnake specimen than in the forms from the Ricardo Pliocene. The crowns in No. 544 seem to be slightly larger. The cement covering is heavier.

This form appears specifically distinct from the Ricardo species and perhaps also from the specimen known from Thousand Creek. It is evidently allied to the latter, as also to a form from the Neohipparion (Hipparion) zone of the North Coalinga region. This species is very close to *Hipparion occidentale* and is not improbably to be referred to that species.

In the collection from the Rattlesnake region of eastern Oregon there is a single lower cheek-tooth, No. 2220, with a rather short, much compressed crown showing in general a close resemblance to *Hipparion leptode* from Thousand Creek. The heavily cemented crown is not greatly worn. It shows more compression than in the Thousand Creek specimen, but is scarcely more than 30 mm. in length, whereas the somewhat worn Thousand Creek specimen evidently reached 70 mm. in length when unworn. It is to be presumed that tooth No. 2220 is a milk molar of the *Hipparion* type like the type of *H. leptode* from Thousand Creek or possibly represents the milk dentition of *H. occidentale.*

Comparative Measurements (in Millimeters) of Teeth

	No. 544, Rattlesnake.	Hipparion leptode, type No. 19414, Thousand Creek.
P$\bar{2}$, antero-posterior diameter	27.2	....
P$\bar{2}$, transverse diameter	13.2	....
M$\bar{1}$, antero-posterior diameter	26.7	....
M$\bar{1}$, transverse diameter	12.9	....
M$\bar{1}$, antero-posterior diameter of metaconid-metastylid column	15.8	....
M$\bar{2}$, antero-posterior diameter	25.9	29 plus
M$\bar{2}$, transverse diameter	10.5	11
M$\bar{2}$, antero-posterior diameter of metaconid-metastylid column	14.4	14.6
M$\bar{2}$, greatest length of crown	57.5 (worn)	66

Hipparion anthonyi Merriam

A very fragmentary specimen consisting of parts of several upper cheek-teeth from U. C. locality 3062 in the Rattlesnake beds represents a *Hipparion* of approximately the size seen in *Hipparion occidentale.* This specimen, No. 22386 (fig. 35, *a* and *b*), differs from those referred to *H. occidentale* in that the enamel folds bordering the fossettes are more numerous, more closely appressed, and sharper. The protocone is comparatively short antero-posteriorly, and approaches a circular cross-section a little more closely in the protocone of *H. occidentale.* As specimen 22386 represents an individual in which the crowns are worn well toward the base, the character of the enamel folds bordering the fossettes has considerable significance, as the folds tend generally to simplify toward the base of the tooth. The shortness of the crown coupled with complexity of enamel folds might be interpreted as indicating that these teeth

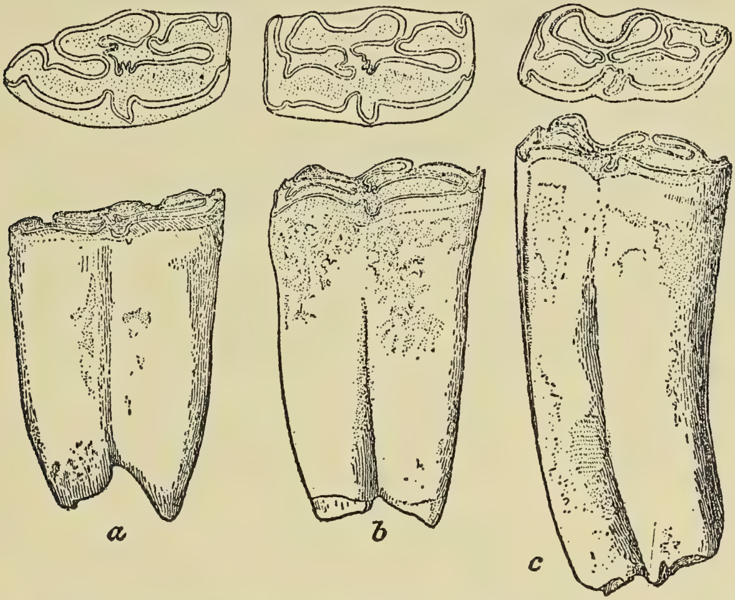

FIG. 34. *Hipparion leptode* Merriam or *Hipparion occidentale* Leidy. Lower cheek-teeth, No. 544 U.C.C.; outer and occlusal views; *a*, $P\bar{2}$; *b*, $M\bar{1}$; *c*, $M\bar{2}$. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

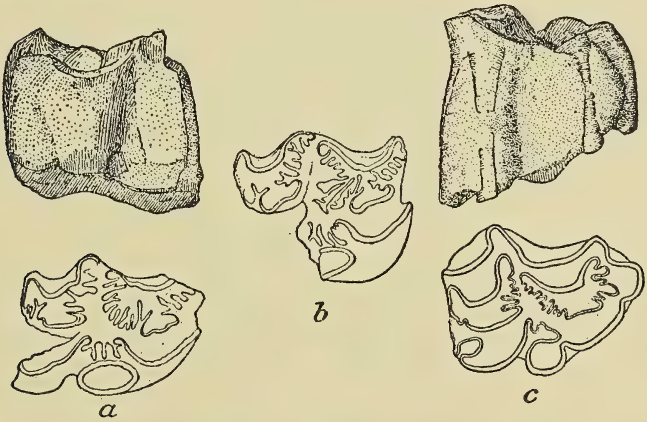

FIG. 35. *Hipparion anthonyi* Merriam. Upper cheek-teeth; lateral and occlusal views; *a* and *b*, No. 22386 U.C.C.; *c*, No. 22362 U.C.C. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

represent the milk dentition, but the crown is, as far as can be determined, much wider than in the milk teeth of *Hipparion.* This species is possibly related to *Hipparion mohavense* of the Ricardo Pliocene or it may represent the upper dentition of *Hipparion anthonyi* of the Ironside region across the Blue Mountains to the southeast of the John Day Valley.

A second individual, No. 22362 (fig. 35c), found with the specimen of *Indarctos* (*?*) *oregonensis* at locality 3058, consists of a single permanent P2, worn down close to the base of the crown. The circular protocone is lightly connected with the protoconule. In spite of the stage of wear, the enamel bordering the fossettes shows very numerous, strongly marked folds. This tooth, which clearly represents the permanent dentition, resembles those of No. 22386 in the extreme complication of the enamel folds in a section of the crown near the base and in the short antero-posterior diameter of the protocone. It probably represents the same species as No. 22386.

RHINOCEROTIDAE

?Teleoceras, near fossiger (Cope)

Remains of rhinoceroses from the Rattlesnake deposits consist of several teeth and include a very fragmentary portion of a mandible in which milk teeth are being replaced by the permanent set. In addition to these specimens there is also available some skeletal material, comprising, among other elements, a lunar, a third metacarpal and metatarsal, and several calcanei.

Specimen 23177, fig. 36*a*, an unworn tooth from locality 3060, represents presumably either P2 or Dm2. The Oregon specimen bears some resemblance in shape to P2, as figured by Leidy and Lucas[24] for *Teleoceras fossiger* from Florida, but it is slightly larger. Although the crochet and anticrochet are well developed in No. 23177, there is no union between them and this separation exists to the base. Two cristae are developed, the anterior of which is the more prominent one. They are closely situated and remain disconnected throughout their length, with each other and with the crochet.

No. 23177 resembles Dm2 closely in size and in presence of the two cristae, but in the specimens of this tooth figured by Leidy and

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[24] Trans. Wagner Free Inst. Sci., vol. 4, pl. 8, fig. 7, 1896.

Lucas[25] the cristae have united with adjoining structures inclosing two small enamel lakes.

M$\underline{3}$, No. 23175 (fig. 36*b*) from the Rattlesnake, is smaller but more worn than the corresponding tooth of *T. fossiger* from Florida, as figured by Leidy and Lucas. In the Rattlesnake specimen the anterior transverse crest is more simple than in the tooth from Florida and the anticrochet is represented by a convexity only.

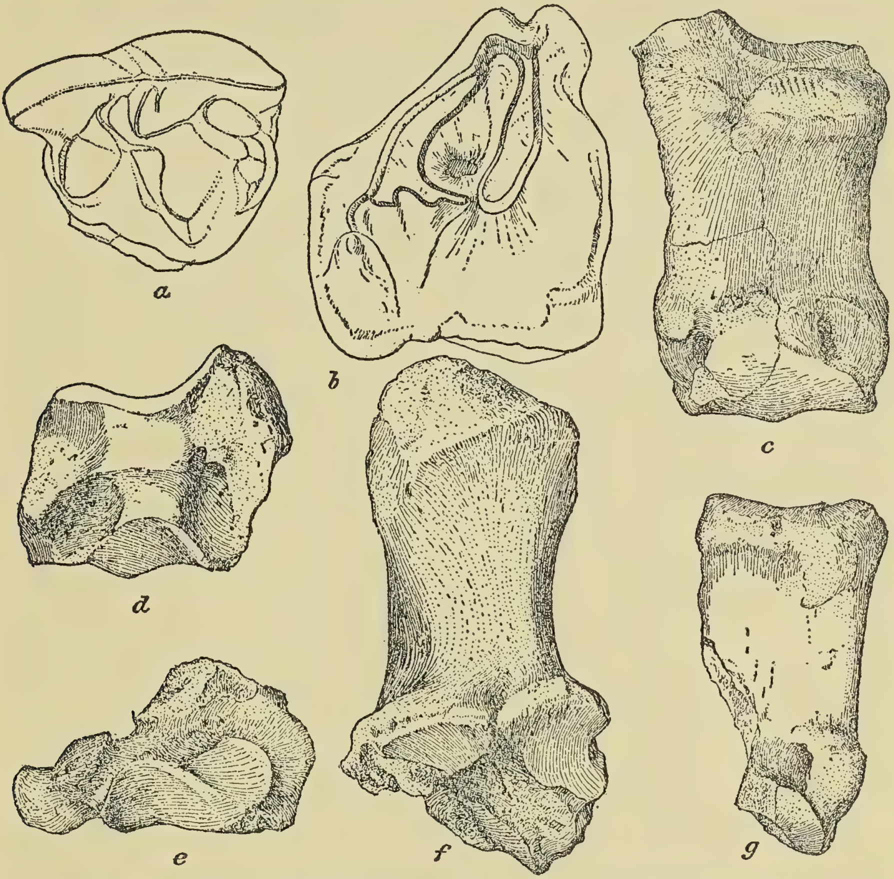

FIG. 36. ?*Teleoceras*, near *fossiger* (Cope). Teeth and skeletal elements; *a*, P$\underline{2}$ or Dm$\underline{2}$, No. 23177 U.C.C.; occlusal view; ×1.0. *b*, M$\underline{3}$, No. 23175 U.C.C.; occlusal view; ×1.0. *c*, metacarpal III, No. 23181 U.C.C.; anterior view; ×0.50. *d*, scaphoid, No. 23860 U.C.C.; antero-internal view; ×0.50. *e*, lunar, No. 23178, ×0.50. *f*, calcaneum, No. 23179 U.C.C.; ×0.50. *g*, metatarsal III, No. 23182 U.C.C.; anterior view; ×0.50. Rattlesnake Pliocene, John Day Valley, Oregon.

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[25] *Op. cit.*, pl. 8, figs. 5 and 13, 1896.

The crochet is, however, well developed. The paracone and parastyle are separated by an open groove which extends the entire height of the crown, thus differing from the Florida specimen in which such separation is absent. The hypocone in the tooth from Oregon is conical and is separated by a shallow notch from the remaining portion of the metaloph.

The Rattlesnake specimen, when compared with the corresponding tooth in No. 22420, a skull of *Teleoceras fossiger* from the Republican River beds of Kansas, is seen to be much smaller. There is a very distinct anticrochet developed, but the crochet is rather small in M$\underline{3}$ of the Kansan form. The tooth from Oregon differs also from the latter in decided separation of parastyle and paracone.

The degree of brachypedy in the Rattlesnake form is comparable to that of *T. fossiger* from the Republican River beds, and there is close similarity between the Oregon and Kansas individuals, not only in the metapodials (figs. 36*c* and *g*) but in other elements of the foot as well. The calcaneum (fig. 36*f*) possesses the long posterior projection characteristic of *T. fossiger*. At the articular end the transverse width in all specimens available decidedly exceeds the antero-posterior diameter.

The rhinoceros known from locality 3068 by a left lunar, No. 23178, fig. 36*e*, and a right scaphoid, No. 23860, fig. 36*d*, was somewhat larger than the adult specimen of *T. fossiger*, No. 22552, from the Republican River and in the collections of the Museum of Palaeontology, University of California.

MEASUREMENTS (IN MILLIMETERS) OF DENTITION

P$\underline{2}$ or Dm$\underline{2}$, No. 23177, greatest antero-posterior diameter	38.5
P$\underline{2}$ or Dm$\underline{2}$, No. 23177, greatest transverse diameter	33.2
M$\underline{3}$, No. 23175, antero-posterior diameter along inner side	45.7
M$\underline{3}$, No. 23175, transverse diameter along anterior crest	52.7

MEASUREMENTS (IN MILLIMETERS) OF FOOT ELEMENTS

Lunar, No. 23178:	
Greatest antero-posterior diameter	88.9
Width (approximate)	43
Dorso-ventral diameter	54.1
Metacarpal III, No. 23181:	
Greatest length	121.9
Width of proximal end	73.5
Width of distal end	67.5

	No. 23179	No. 23180	
Calcaneum:			
Total length	152.1	....	
Antero-posterior diameter of articular end	56.2	65.7	
Transverse diameter of articular end	....	86.2	
Metatarsal III, No. 23182:			
Greatest length (approximate)			103
Transverse diameter of proximal end			55.2
Antero-posterior diameter of proximal end			41

SUIDAE

Prosthennops? sp.

Most of the material pertaining to the peccary was collected at locality 3060 in Rattlesnake gravels and tuffs, and consists of fragmentary parts of jaws and of the dentition. Among the incomplete series of teeth secured there are very often deciduous molars, thus indicating, seemingly, that the band of peccaries whose remains accumulated at locality 3060 consisted of many relatively young individuals.

A fragmentary specimen of the right maxillary, No. 23862 (fig. 37), bears three deciduous molars and the first permanent molar. The milk teeth are much worn. The two anterior teeth of the deciduous set have not become molariform, a character which has been acquired, however, by the third tooth. The former teeth resemble corresponding teeth in *Platygonus*. Dm$\underline{2}$ and Dm$\underline{3}$ possess each a single cusp on the anterior half and two cusps arranged in transverse row on the posterior half of the tooth. In the type of *Prosthennops crassigenis* the teeth are greatly worn and adequate comparison can not be made therefore between M$\underline{1}$ of the Rattlesnake specimen and the corresponding tooth in Gidley's species. The facial pit of the maxillary, situated above the deciduous teeth, is deeply formed in No. 23862.

A symphyseal part of a mandible, No. 23861 (fig. 38), does not possess the canine and incisor teeth in a good state of preservation. In this specimen three incisors are present in each ramus, the medial two well developed and the lateral one rudimentary. The diastema between I$\overline{3}$ and the canine is much longer than in *Tayassu*. The diastema behind the canine is also long, having an extent equivalent to that in *Platygonus*. It is fully as long, if not longer, than that in the Snake Creek specimen, determined by Matthew and Cook[26] as

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[26] W. D. Matthew and H. J. Cook, Bull. Amer. Mus. Nat. Hist., vol. 26, pp. 389–391, fig. 13, 1909.

Prosthennops cf. *crassigenis*. Two mental foramina are present, one below the anterior border of the canine and near the symphyseal line, the other below and toward the end of the diastema. There is no ventral keel in No. 23861.

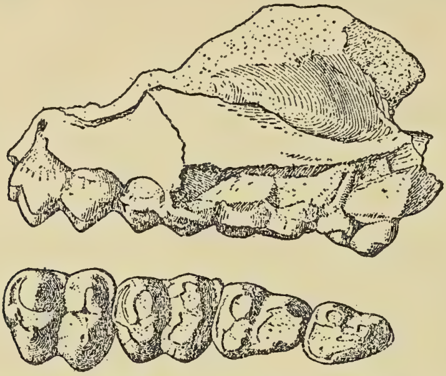

Fig. 37. *Prosthennops?* sp. Fragment of maxillary with teeth, No. 23862 U.C.C.; lateral and occlusal views; ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

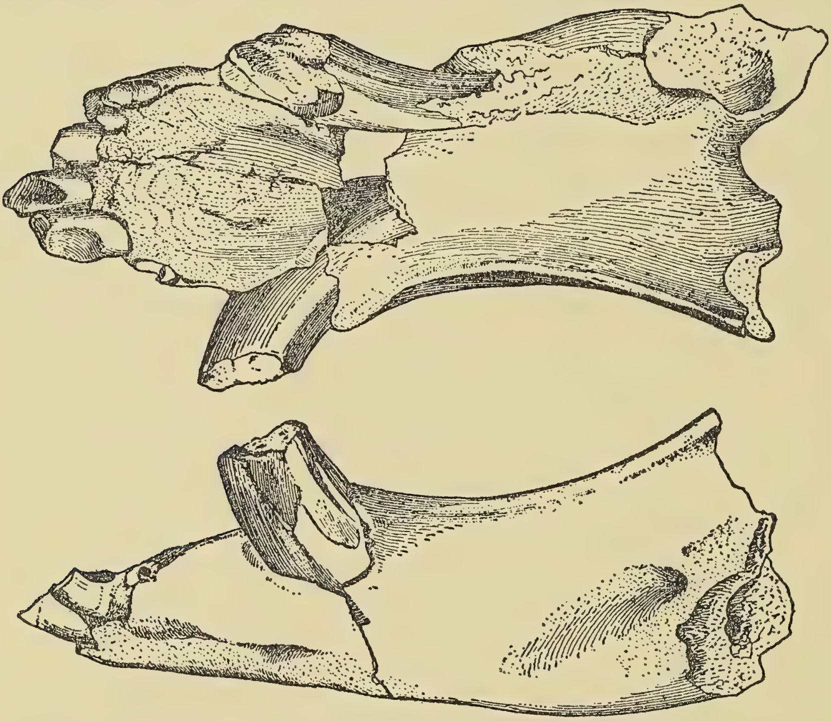

Fig. 38. *Prosthennops?* sp. Symphyseal part of mandible, No. 22861 U.C.C.; dorsal and lateral views; ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

The inferior canine in the Rattlesnake species, No. 23868, is of triangular outline with outer face slightly convex, inner face flattened, and posterior face slightly concave. This tooth when unworn shows a distinct recurvature at the tip.

M$\bar{1}$ and M$\bar{2}$ in specimen 23863 (fig. 39*a*) are close in size to corresponding teeth in the fragmentary ramus of the mandible from the Snake Creek beds referred provisionally by Matthew and Cook to *Prosthennops* and compared with the species *crassigenis*. The lower jaw as represented by the fragment from the Rattlesnake compares favorably in size with the Snake Creek material, but the former belongs to a younger individual. A distinct but shallow groove exists along the inner side and above the lower border of the Oregon specimen as in the Recent *Tayassu*. M$\bar{1}$ in No. 23863 is smaller than the corresponding tooth in the jaw from the Snake Creek beds referred by Matthew[27] to *Prosthennops serus*, slightly more so in antero-posterior diameter, decidedly more so in transverse diameter. M$\bar{2}$ is of same length but decidedly narrower transversely than the corresponding tooth in the Snake Creek species, *P. serus*. The occlusal pattern of the two teeth of No. 23863 and that of the teeth of *P. serus* seem fairly close, but in the Oregon form the cusps are slightly higher.

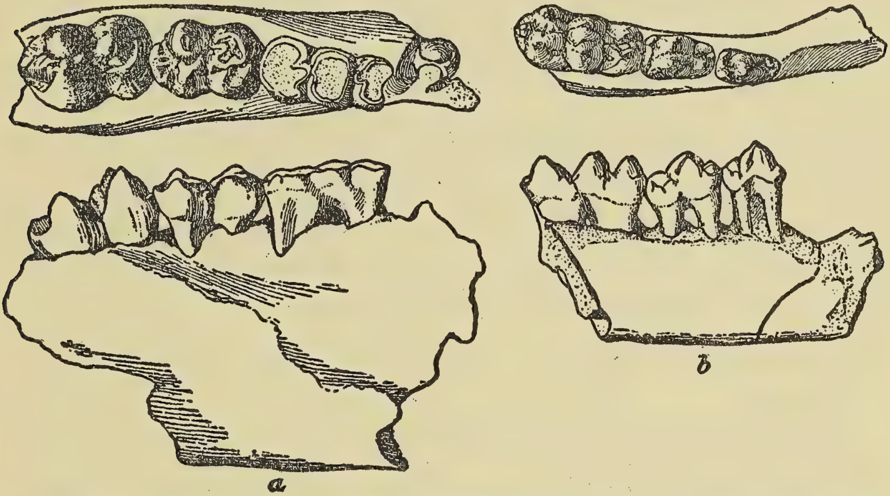

FIG. 39. *Prosthennops* sp. Mandibular fragments with teeth; lateral and occlusal views; *a*, No. 23863 U.C.C., functional teeth include Dm$\bar{4}$, M$\bar{1}$, and M$\bar{2}$; *b*, No. 23864 U.C.C., Dm$\bar{2}$, Dm$\bar{3}$, and Dm$\bar{4}$. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

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[27] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 214–215, fig. 15, 1918.

Peccaries appear to have been better represented in the Rattlesnake fauna than in the Pliocene assemblage of mammals found in the Thousand Creek beds of Nevada. The symphyseal fragment described by Merriam[28] from the latter deposits resembles No. 23861 from the Rattlesnake in possessing the full complement of incisor teeth. The differences which distinguish the Thousand Creek form are very slight and rest in (1) greater width anterior to canine teeth (2) larger I$\bar{3}$, (3) shorter interspace between alveoli for I$\bar{3}$ and canine, and (4) larger anterior mental foramen.

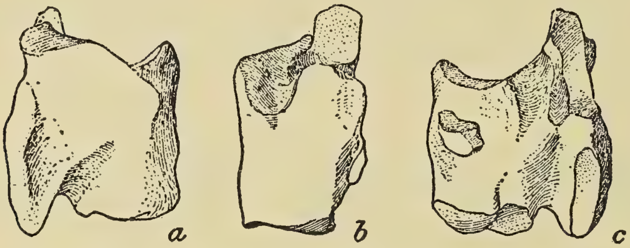

FIG. 40. *Prosthennops?* sp. Cuboid, No. 23865 U.C.C.; *a*, anterior view; *b*, outer view; *c*, inner view. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

MEASUREMENTS (IN MILLIMETERS) OF MATERIAL REFERRED TO PROSTHENNOPS? SP.

No. 23862:	
Length of tooth series, Dm$\underline{1}$ to M$\underline{1}$ inclusive	49.8
Dm$\underline{2}$, antero-posterior diameter	10
Dm$\underline{2}$, greatest transverse diameter	7.4
Dm$\underline{3}$, antero-posterior diameter	12.7
Dm$\underline{3}$, greatest transverse diameter	9.7
Dm$\underline{4}$, antero-posterior diameter	12.8
Dm$\underline{4}$, greatest transverse diameter across anterior half	11.2
M$\underline{1}$, antero-posterior diameter	14
M$\underline{1}$, greatest transverse diameter across anterior half	12
No. 23863 (possibly same individual as No. 23862):	
Dm$\bar{4}$, antero-posterior diameter	17.9
Dm$\bar{4}$, transverse diameter posteriorly	9.3
M$\bar{1}$, antero-posterior diameter	16.6
M$\bar{1}$, transverse diameter posteriorly	11
M$\bar{2}$, antero-posterior diameter	18.3
M$\bar{2}$, transverse diameter posteriorly	12.8
Depth of lower jaw between M$\bar{1}$ and M$\bar{2}$ measured normal to tooth row	34.2
Thickness of lower jaw below M$\bar{1}$	17.4

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[28] J. C. Merriam, Univ. Calif. Publ. Bull. Dept. Geol., vol. 6, pp. 272–275, fig. 54, 1911.

No. 23864:	
Length of lower deciduous series ($\mathrm{Dm}\bar{1}$ to $\mathrm{Dm}\bar{3}$ inclusive)	37.8
$\mathrm{Dm}\bar{2}$, antero-posterior diameter	9
$\mathrm{Dm}\bar{2}$, transverse diameter posteriorly	4.8
$\mathrm{Dm}\bar{3}$, antero-posterior diameter	10.7
$\mathrm{Dm}\bar{3}$, transverse diameter posteriorly	6.2
$\mathrm{Dm}\bar{4}$, antero-posterior diameter	18.3
$\mathrm{Dm}\bar{4}$, transverse diameter posteriorly	8.8
No. 23867:	
Superior canine, antero-posterior diameter at base of crown (approximate)	13.3
Superior canine, transverse diameter at base of crown	7.3
Superior canine, length of crown measured along anterior border	27.5
No. 23866:	
Inferior canine, antero-posterior diameter at base of crown	13
Inferior canine, transverse diameter at base of crown	8
No. 23861:	
Length of symphysis of mandible in horizontal line	86.9
Width of symphyseal part of mandible anterior to alveoli for canine teeth	29
Vertical depth of symphysis at posterior end	20.3
Length of diastema between alveoli for $\mathrm{I}\bar{3}$ and canine	8.3
Right cuboid, No. 23865:	
Antero-posterior diameter	22.5
Transverse width anteriorly	16
Proximo-distal diameter anteriorly	21.3

?Platygonus rex Marsh

A very large peccary has been described by Professor Marsh[29] from three molar teeth of large size obtained from deposits presumed to be Pliocene occurring in eastern Oregon. L. S. Davis, who was employed by Professor Marsh as collector in the John Day region, recalls securing what he believes to be the type specimen of this species in the Rattlesnake gravels of the type area.

According to Marsh[29] the peculiar characters of *Platygonus rex* are found in its large size, and in the fact that the crowns of the cheek-teeth are composed of well-rounded conical tubercles, few in number. The figures of the type specimen published by Marsh represent a form in which the crowns of the cheek-teeth exhibit a simplicity of the tubercles. In these teeth no transverse ridges or lophs are formed.

Marsh's species presumably represents a form in or near *Prosthennops*. In certain characters it verges towards *Mylohyus*, but in this second genus intermediate tubercles are developed to a much greater extent than in Marsh's species from the Rattlesnake.

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[29] O. C. Marsh, Amer. Jour. Sci., ser. 3, vol. 48, p. 273, 1894.

J. W. Gidley[30] has compared *Platygonus texanus* with *P. rex* and indicates differences. As to the age of the latter form Gidley states: "Marsh gives the horizon as Pliocene, but it is almost certainly Upper Miocene."

Of the various dicotyline forms known in the Tertiary of the Pacific Coast and Great Basin provinces the one most closely resembling the type of Marsh's *Platygonus rex* is that represented by two lower molar teeth from the Etchegoin formation[31] on the western border of the Great Valley of California. Specimen 21360 of the upper Etchegoin fauna shows dimensions and form closely similar to $M\overline{3}$ of Marsh's type of *Platygonus rex*. It is doubtful whether the two forms are specifically identical, but they appear to be closely related.

COMPARATIVE MEASUREMENTS (IN MILLIMETERS)

	Platygonus rex.	No. 21360, Etchegoin formation.
$M\overline{3}$, greatest antero-posterior diameter	27.4	27.2
$M\overline{3}$, transverse diameter	16	15.9

CAMELIDAE

Although some parts of the dentition are available, the greater portion of the camel material from the Rattlesnake beds consists of skeletal elements. Practically all the remains are to be referred to the larger types, such as perhaps would be represented by *Pliauchenia* and *Alticamelus*.

Several upper and lower molar teeth are available. At locality 3068 $M\underline{1}$ and $M\underline{2}$ were found associated together with a lower molar, and presumably the three teeth belong to the same individual, No. 23857. In the upper teeth (fig. 41) the anterior lobe, particularly that in $M\underline{2}$, is decidedly ridged externally. The following measurements (in millimeters) of these teeth have been taken at the base of the crown:

Length from anterior end of $M\underline{1}$ to posterior end $M\underline{2}$	68.4
$M\underline{1}$, antero-posterior diameter	32.7
$M\underline{1}$, transverse diameter through posterior lobe	30.4

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[30] J. W. Gidley, Bull. Amer. Mus. Nat. Hist., vol. 19, p. 479, footnote, 1903.

[31] J. C. Merriam, Trans. Amer. Philos. Soc., vol. 22, pt. 3, p. 36, figs. 40*a* and 40*b*, 1915.

M$\underline{2}$, antero-posterior diameter	38.3
M$\underline{2}$, transverse diameter through anterior lobe	33
Lower molar, antero-posterior diameter	36.1
Lower molar, transverse diameter	26.3

A somewhat smaller and less worn molar tooth, No. 23856, from the type locality of the Rattlesnake, has the ridges on the outer walls of paracone and metacone even more prominently developed than in No. 23857. The measurements in millimeters of this specimen are: M$\underline{2}$?, antero-posterior diameter at base of crown, 37.4; M$\underline{2}$?, transverse diameter through anterior lobe, 27.

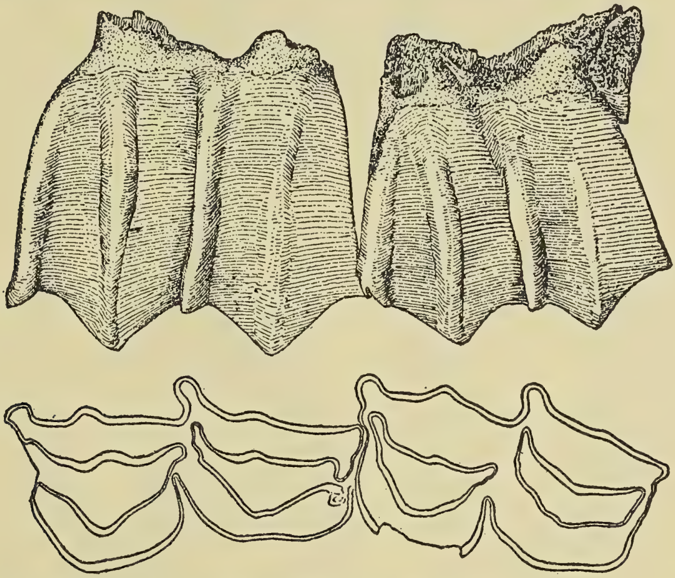

Fig. 41. *Pliauchenia?* or *Alticamelus?* sp. M$\underline{1}$ and M$\underline{2}$, No. 23857 U.C.C.; lateral and occlusal views; ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

Limb elements.—A cannon bone of the posterior limb is preserved by a considerable part of the proximal half and is comparable in size to the largest of the posterior metapodials from Ricardo and referred tentatively to *Pliauchenia* or *Alticamelus*. This specimen, No. 23853, is shown in figure 42, *a* and *b*.

There are at least two types of astragali belonging to the camels, one of which, No. 23854, is similar in size and shape to specimens from the Ricardo Pliocene that have been referred tentatively to *Alticamelus*. A second type of astragalus is apparently indicated by specimen 23861 which is somewhat smaller than No. 23854 and may be tentatively determined as belonging to *Pliauchenia* or *Alticamelus*.

The sustentacular portion of a calcaneum, No. 23858, from the Rattlesnake deposits is of same size as that in specimen No. 21567 from the Ricardo beds, referred to *Alticamelus* or *Pliauchenia?*.

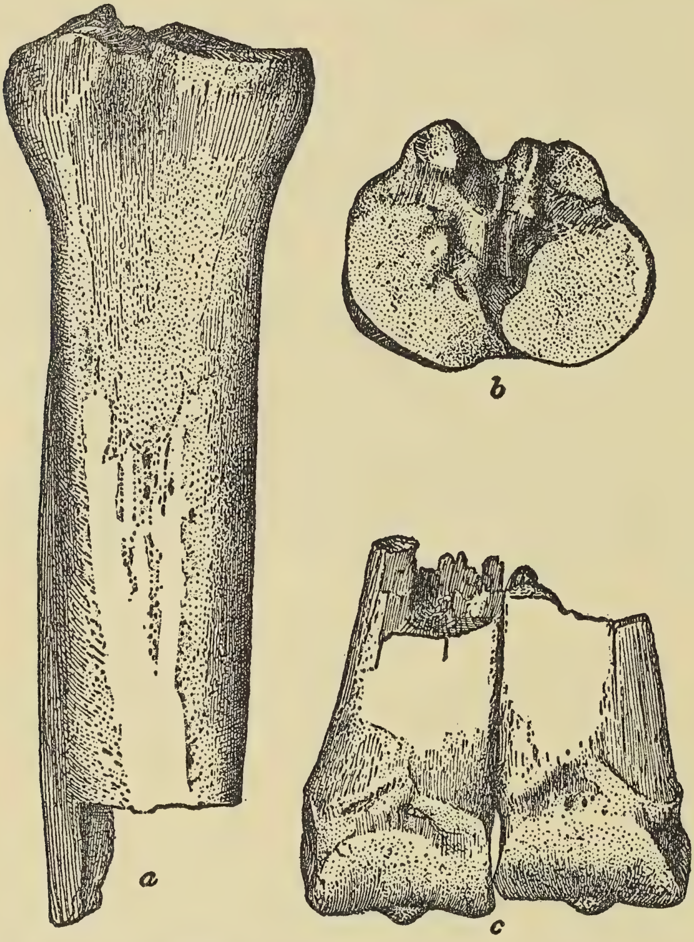

Fig. 42. *Pliauchenia?* or *Alticamelus?* sp. Cannon bones; *a*, posterior cannon bone, No. 23853 U.C.C., anterior view; *b*, No. 23853 U.C.C., proximal view; *c*, No. 26790 U.C.C., anterior view. ×0.50. Rattlesnake Pliocene, John Day Valley, Oregon.

Proximal phalanges have not been found as abundantly in the Rattlesnake beds as in the Ricardo deposits. The best preserved phalanx approximates in size specimens from the Ricardo.

Comparative Measurements (in Millimeters) of Limb Elements

	Rattlesnake, No. 23853	Ricardo, No. 23118
Posterior cannon bone:		
Width of proximal end	80	81.6
Greatest antero-posterior diameter of proximal end	64.4	63

	Rattlesnake, No. 23855	Ricardo, No. 21567
Calcaneum:		
Depth of sustentaculum	81.6	83.5
Width at base of tuber calcis	58.7	59

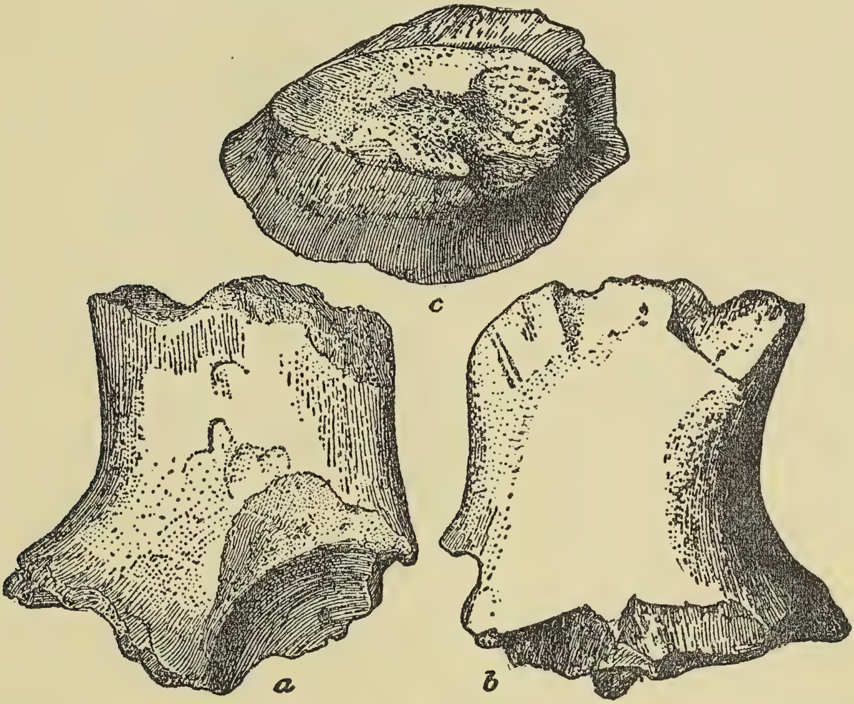

Fig. 43. *Sphenophalos* sp. Horn-core, No. 22428 U.C.C.; *a,* outer view; *b,* inner view; *c,* dorsal view. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

BOVIDAE

Sphenophalos sp.

Specimen 22428, found by the 1916 expedition at U. C. locality 3045 in the Rattlesnake formation, represents the basal portion of the horn-core and the posterior-superior region of the orbit of an antelope of the *Sphenophalos* type (fig. 43). In cross-section of the horn-core, No. 22428 is not identical with any of the few specimens of adult *Sphenophalos* from Thousand Creek, but its form falls well within the limits of variation of the Thousand Creek material.

While it is not possible to demonstrate that this Rattlesnake specimen is to be referred to the Thousand Creek species, it is evidently a form closely related to it, if it is not identical with it. This is the only known occurrence of a horn-core of any of the several types of Thousand Creek antelopes outside the limits of the typical Thousand Creek beds.

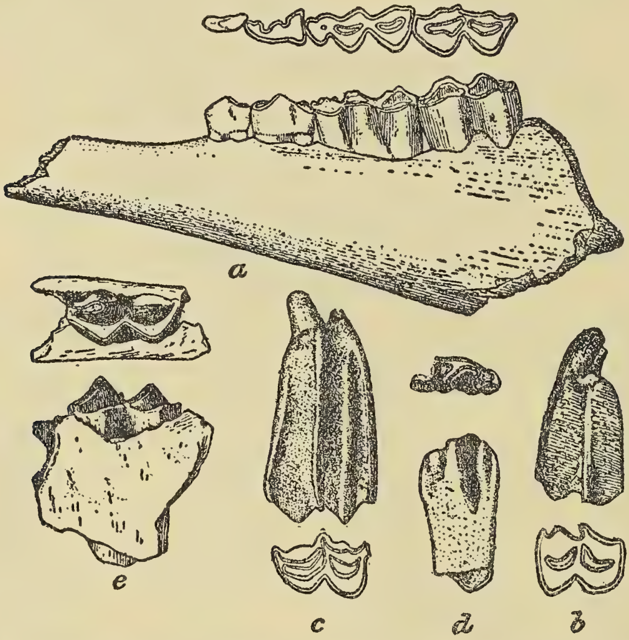

Fig. 44. *Ilingoceros or Sphenophalos?* sp. Fragment of lower jaw and teeth; *a*, jaw with deciduous teeth and $\mathrm{M}\overline{1}$, No. 22426 U.C.C.; *b*, upper molar, No. 22435 U.C.C.; *c*, upper molar, No. 22433 U.C.C.; *d*, $\mathrm{P}\overline{4}$ or $\mathrm{P}\overline{3}$, No. 22446 U.C.C.; *e*, lower molar, No. 22445 U.C.C. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

Ilingoceros or Sphenophalos? sp.

Several specimens of skeletal elements and teeth from the Rattlesnake represent antelope forms approaching some of the Thousand Creek types referred to *Ilingoceros* and *Sphenophalos.* With the scanty material available it is difficult to make an exact determination.

An astragalus, No. 22434 (fig. 45*d*), from locality 3057, associated with an antelope upper cheek-tooth, has the size and the peculiarities of form characterizing small Thousand Creek antelope astragali referred to *Sphenophalos* or *Ilingoceros*, possibly representing the first of these two genera. In this specimen there is a well-developed flange below the inner trochlear ridge and the posterior end of this ridge terminates in a marked inferior process extending almost at right angles to the antero-posterior plane of the astragalus. The inner trochlear articular surface which extends out upon this inferior process does not bend around beneath the astragalus sufficiently far to turn forward inferiorly as it does in *Antilocapra*. Both the character of this inner flange and that of the posterior process described are distinctive characters of Thousand Creek antelopes. Among the Thousand Creek forms there are two types of astragali: a larger and somewhat wider form in which the flange below the inner side of the trochlea is low, and a smaller narrower type with less pronounced inner flange. The former is possibly to be associated with the large *Sphenophalos* or *Ilingoceros* and the latter with the small *Ilingoceros* or a small form (No. 22430) presumed to lead to *Sphenophalos*. In both of these types the characteristic peculiar process below the inner posterior end of the inner trochlear ridge is present. Specimen 22434 presumably represents the larger of the two Thousand Creek forms. The measurements in millimeters of No. 22434 are as follows: Greatest length, 34.5; greatest width, 21.9.

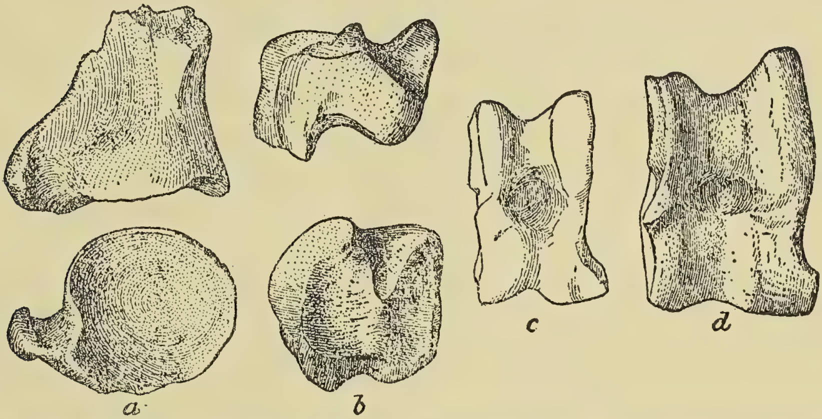

FIG. 45. *Ilingoceros* or *Sphenophalos?* sp. Skeletal elements; *a*, fragment of scapula, No. 22432 U.C.C.; *b*, naviculo-cuboid, No. 22436 U.C.C.; *c*, astragalus, No. 22443 U.C.C.; *d*, astragalus, No. 22434 U.C.C. ×1.0. Rattlesnake Pliocene, John Day Valley, Oregon.

An astragalus, No. 22443 (fig. 45*c*), from locality 3045, is much smaller than specimen 22434 and is also narrower transversely. It is of approximately the same size as numerous antelope astragali of the smaller and narrower Thousand Creek type, presumably representing one of the small species of *Ilingoceros* or possibly a small form of *Sphenophalos*. This specimen is slightly narrower than the small Thousand Creek form, but the difference may not indicate more than a specific separation. Small antelope astragali from the Orinda-Pinole Tuff Pliocene at Pinole, California, closely approach the Rattlesnake specimen 22443 in size, and resemble this form in being relatively narrow. In narrowness the Pinole forms may even exceed the Rattlesnake specimen. The measurements in millimeters of astragalus, No. 22443, are as follows: Greatest length, 27; greatest width, 16.9.

The distal end of a small scapula, No. 22432 (fig. 45*a*), is not distinguishable from the corresponding region of the scapula of a small Thousand Creek antelope, No. 11892, referred to *Ilingoceros*. A naviculo-cuboid, No. 22436 (fig. 45*b*), from the same locality as the scapula, also corresponds in size and form to small antelope naviculo-cuboid elements found at Thousand Creek and referred to *Ilingoceros*.

A tooth, No. 22435 (fig. 44*b*), found associated with astragalus 22434, corresponds to an upper molar of *Ilingoceros* or *Sphenophalos*.

A lower jaw with milk dentition and with M$\bar{1}$ in function, No. 22426 (fig. 44*a*), represents an antelope having approximately the size of the small forms of the Thousand Creek fauna. M$\bar{1}$ shows form and dimension close to those of specimens from Thousand Creek. In the milk dentition the characters are more advanced than those in *Merycodus* and in some respects more advanced than in *Capromeryx*. The teeth are larger and longer crowned than in *Merycodus* and the anterior lobe of Dm$\bar{4}$ is larger. Compared with *Capromeryx* the crowns of the milk teeth are not longer, but the anterior lobe of Dm$\bar{4}$ is larger. The inner side of Dm$\bar{3}$ possesses a postero-internal fold not present in *Capromeryx*, and there is an antero-internal fold on Dm$\bar{3}$ which is only faintly marked on the corresponding teeth of the Rancho La Brea *Capromeryx*. In *Antilocapra* Dm$\bar{4}$ is not larger than in No. 22426, and the anterior lobe is relatively smaller. In *Antilocapra* M$\bar{1}$ has dimensions and form near those of No. 22426. Possibly the anterior lobe of M$\bar{1}$ in No. 22426 can be distinguished from that of *Antilocapra* by stronger inner curvature at the anterior end. The form of the mandible in No. 22426 in some respects approaches that in *Capromeryx* more closely than it does the outline of the only known antelope mandible specimen from the Thousand Creek beds. In the Thousand Creek specimen No. 22440, the ramus in the region of the diastema narrows comparatively little toward the anterior end. In *Capromeryx* the region of the diastema is relatively short and its height diminishes rather rapidly toward the anterior end. In Rattlesnake specimen No. 22426, the portion of the ramus in the region of the diastema is relatively narrow and slender. This may be due to a relatively early stage of development or it may be a distinguishing character. Young individuals of *Antilocapra* show relative slenderness in the region of the diastema, but no specimens have been examined in which the forward taper is as marked as in the Rattlesnake specimen.

A lower molar, No. 22445 (fig. 44*e*), associated with the small antelope astragalus No. 22443, resembles M$\overline{1}$ of mandible 22426 in form, but represents a somewhat larger animal. It is near the size of certain small lower cheek-teeth of antelopes from Thousand Creek but as in No. 22426 it may be narrower transversely and shows somewhat greater anterior prolongation of the anterior lobe. A portion of a lower P$\overline{4}$ or P$\overline{3}$, No. 22446, has a crown-pattern approaching that of *Antilocapra* in complication.

A large M$\underline{1}$, No. 22433 (fig. 44*c*), of an antelope, associated with a small scapula, No. 22432, and naviculo-cuboid, corresponds approximately in size and form to a tooth, No. 12605, from the Thousand Creek. In the Rattlesnake form the outer rib on the paracone seems more strongly marked. There is possibly a small difference in this character between No. 22433 and the Thousand Creek form, but the latter is nearer to No. 22433 than is *Antilocapra*.

COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF DENTITION

	Ilingoceros or Sphenophalos, No. 22426.	Capromeryx, No. 19977.	Antilocapra, No. 8299, U. C. Mus. Vert. Zool.
Dm$\overline{2}$, antero-posterior diameter	5.5	4.2	....
Dm$\overline{2}$, transverse diameter	2.4	2	....
Dm$\overline{3}$, antero-posterior diameter	7.8	6	7.2
Dm$\overline{3}$, transverse diameter	4.1	2.7	3.7
Dm$\overline{4}$, antero-posterior diameter	14.5	9.6	12.1
Dm$\overline{4}$, transverse diameter	5.4	4	4.6
M$\overline{1}$, antero-posterior diameter	12.7	9.3	11.8
M$\overline{1}$, transverse diameter	5.6	4.2	6.1

A HYAENARCTID BEAR FROM THE LATER TERTIARY OF THE JOHN DAY BASIN OF OREGON

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History of Discovery and Identification of Material.................. 663
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Introduction

In the course of field investigations on the Mascall and Rattlesnake deposits and faunas of the John Day Basin of eastern Oregon, conducted by Chester Stock and C. L. Moody during 1916,[1] fragmentary material of a hyaenarctid type was discovered at University of California collecting locality 3042. The specimen was described in 1925 by John C. Merriam, Chester Stock and C. L. Moody.

Locality 3042 was visited again during the summer of 1926. Charles W. Merriam, a member of the party in search of mammalian remains at this locality, discovered several hyaenarctid teeth and fragments. Study of this new material has shown that it represents the individual found in 1916. The additional remains furnish valuable information relating to the Tertiary bears of North America.

Location of Material

The locality (U. C. C. locality 3042) at which the hyaenarctid remains were found is that at which a number of interesting specimens have been obtained by expeditions from the University of California in 1900 and 1916. At this station there have been secured

By John C. Merriam and Chester Stock. *Carnegie Institution of Washington Publication No. 346*, paper III, pp. 39–44, pl. 1, November 1, 1927.

[1] Carnegie Inst. Wash. Pub. No. 347, pp. 65–66, fig. 17, 1925.

a number of specimens of *Hipparion*, belonging to forms related to the species *H. sinclairi* and *H. occidentale*.

Locality 3042 occurs near the lower boundary of the NW¼ and NE¼ of Sec. 36, T. 12S., R. 25E., Willamette Base and Meridian. The locality is situated on the south slope of a ridge with elevation of 3240 feet, shown on the topographic map known as the Picture Gorge Special, Oregon, soon to be published by the U. S. Geological Survey, and is approximately 3 miles southwest of the Mascall Ranch.

The south face of the 3,240-foot ridge at locality 3042 presents exposures of white tuffaceous sediments overlain by coarse gravels and brownish tuffs or clays. The deposits appear at first sight to represent two distinct accumulations, heretofore presumed to be the Mascall Miocene at the bottom of the exposed section and the Rattlesnake Pliocene at the top. The tentative view has been entertained that the presumed Mascall deposits represent a higher horizon than that occurring at the type section of the Mascall, near the Mascall Ranch.

Further investigation of the geologic relations of the later Tertiary formations at this locality and in the adjacent area by John P. Buwalda has cast some doubt upon the original assumption. There appears to be a possibility that in the section under consideration the separation of the lower and the upper beds is more apparent than real and that the entire section exposed at locality 3042 may be Rattlesnake in age. The lower portion of the section may represent the Rattlesnake formation, although differing somewhat in its lithological characters from the typical Rattlesnake. In view of the fact that a study of the geology and palaeontology of the Picture Gorge sheet is now in progress it does not appear desirable to express a definite opinion as to the age of the deposits at locality 3042 until the critical studies in the field have been concluded.

History of Discovery and Identification of Material

The hyaenarctid material found by Stock and Moody at locality 3042 in 1916 consisted of a maxillary fragment with a carnassial tooth and the alveolus for $\underline{P3}$, and a root of a molar tooth, No. 22461, University of California Collection. $\underline{P4}$ lacked a portion of the protocone. The specimens discovered by Charles W. Merriam in 1926 included $\underline{M1}$ and $\underline{M2}$ and several fragments of teeth. In each case the specimens were found lying on the white tuffaceous sediments distinctly below the brownish beds with coarse gravels which are exposed in the upper portion of the section. There is reason for believing that the teeth were originally embedded in the white deposits.

The preservation of the remains found in 1926 corresponds almost exactly to that of the material collected in 1916. When the upper carnassial and associated material secured by Stock and Moody and the upper molars and fragments of teeth discovered by Charles W. Merriam were brought together, it was found that the outer anterior root, broken away and missing in $M\underline{1}$ secured in 1926, had been collected with the carnassial in 1916. The root fits to $M\underline{1}$ perfectly. Furthermore, a fragment of crown in the collection made by Charles W. Merriam was identified as a portion of the protocone missing in the carnassial collected by Stock and Moody. The fragment fits perfectly in position below the root supporting this cusp in $P\underline{4}$.

Recognition of a missing part of the specimen collected in 1926 in the collections secured in 1916 and the identification of a fragment of a tooth crown found during the past summer as a part belonging to the carnassial collected ten years ago leave no doubt that the teeth were obtained from the same spot and that they are parts of the same individual. The fact that the characteristics of the two upper molars and of the fourth upper premolar were before their comparison suggested to indicate the same type of animal, and that more careful study shows the same relationship, gives every reason for considering these teeth as representing the same individual.

As a result of the study of the material secured in 1916 the form occurring at locality 3042 was tentatively referred to the Ursidae and was presumed to be a member of the *Indarctos-Hyaenarctos* group.

Description of Material

Indarctos, near oregonensis Merriam, Stock and Moody

(Plate I)

Carnegie Inst. Wash. Pub. No. 347, pp. 65–66, fig. 17, 1925.

$P\underline{4}$, as described by Merriam, Stock and Moody, resembles *Indarctos oregonensis* in its general characters, but differs in the somewhat smaller size of the protocone and in the different form of the parastyle. The tooth is also smaller and less massive than in the type of *I. oregonensis.* The parastyle in P$\underline{4}$ of the type of *I. oregonensis* seems to have been more distinctly separated from the paracone and is probably more nearly conical in shape. With the discovery of the missing part of the protocone (deuterocone) in P$\underline{4}$, the size of this cusp relative to the size of the tooth is seen to be quite comparable to that in the carnassial of *I. oregonensis.*

In other respects P$\underline{4}$ in No. 22461 is distinctly of the type of *Indarctos oregonensis* and differs from *Arctotherium* in that the protocone (deuterocone) is situated in advance of the cleft between paracone and metacone, and its anterior border extends as far forward as the cleft between paracone and parastyle. In *Arctotherium* the protocone is situated much farther back and its anterior border reaches only slightly in advance of the cleft between paracone and metacone.

Of the two molar teeth found by Charles W. Merriam, M$\underline{1}$ is of the *Hyaenarctos* type with high, relatively simple and laterally slightly compressed paracone and metacone and with simple protocone and hypocone. There is no division of the protocone or hypocone as in *Arctotherium* and there are no accessory tubercles in the middle of the occlusal surface. There is a faint tubercle on the cingulum in front of the paracone suggesting an incipient parastyle as in *Arctotherium*, but it is not more strongly marked than in certain other bears. The inner anterior border of the crown tends to make this end of the tooth rather angular and prominent, in which respect No. 22461 is like the California species of *Arctotherium.* M$\underline{1}$ is 3-rooted as in *Arctotherium simum.* The largest root supports the inner side. Of the two outer roots that supporting the metacone is the larger.

M$\underline{1}$ is narrower transversely than in any species of *Hyaenarctos* known to the writers. The dimensions are most nearly approached in *Indarctos* (*Hyaenarctos*) *punjabiensis* Lydekker. The proportions of M$\underline{1}$ approached in some respects those of *Arctotherium haplodon* or of the corresponding tooth in *Tremarctos.*

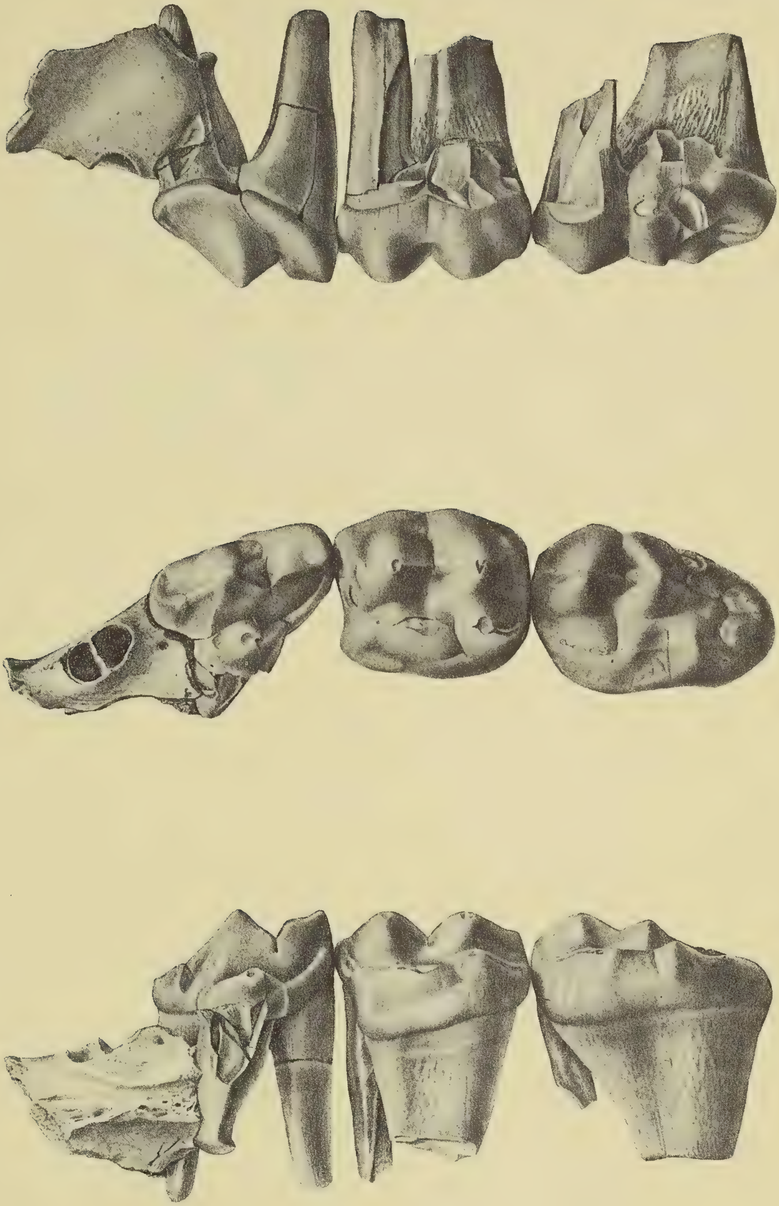
M$\underline{2}$ corresponds more nearly to the structure of *Indarctos oregonensis* than to any other of the forms in the *Hyaenarctos* group. It approaches in certain respects the characters of *Arctotherium*, especially in the size of the heel. On the whole, however, the characters are those of *Hyaenarctos* rather than of *Arctotherium* as indicated by the lower cusps and the absence of intermediary cusps or corrugations and the general simplicity of the occlusal surface of the tooth. M$\underline{2}$ is 3-rooted, with the roots comparable in size to those in *I. oregonensis*. The two outer roots are separated slightly more than in the latter form.

M$\underline{2}$ is smaller than in the type of *Indarctos oregonensis*. It is also relatively narrower and the heel seems larger. M$\underline{2}$ in No. 22461 may show a little less narrowing across the metacone than in the type of *Indarctos oregonensis*. The narrowing of the heel region is also less marked in No. 22461 than in the type of *Indarctos oregonensis*. The development of the heel in No. 22461 approaches that of the arctotheres and of the fairly specialized bears of the *Ursus* group. The stage of development of this character is unlike that in any other member of the *Hyaenarctos* group. The only comparable form in this group of the old world is *Indarctos salmontanus* Pilgrim of the Salt Range.

No. 22461 represents an individual of the *Indarctos-Hyaenarctos* group. It is probably the most highly specialized member of the group thus far known.

MEASUREMENTS OF NO. 22461

	mm.
P$\underline{4}$, anteroposterior diameter measured along outer side	26.7
P$\underline{4}$, width across protocone	19.3
P$\underline{4}$, anteroposterior diameter of paracone at base	13
M$\underline{1}$, greatest anteroposterior diameter	26.7
M$\underline{1}$, greatest transverse diameter	22.9
M$\underline{2}$, greatest anteroposterior diameter	32.4
M$\underline{2}$, anterior end of tooth to posterior end of paracone	12.6
M$\underline{2}$, anterior end of tooth to middle of metacone	17.4
M$\underline{2}$, width of tooth across paracone (approximate)	23.6
M$\underline{2}$, width of tooth across metacone	22



Indarctos, near *oregonensis*, Merriam, Stock and Moody. Superior teeth, No. 22461 U. C. C. Outer, occlusal and inner views, ×0.9. Rattlesnake Pliocene or Mascall Miocene, John Day Basin, eastern Oregon.

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